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Morphology, Function, and Phylogenetic Significance of Pubic Nipples in Bats (Mammalia: Chiroptera)

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ABSTRACT

Pubic nipples (abdominal nipples located on the ventral body wall near the pubes) are present in only a few bat taxa. Examination of 1723 individuals representing 206 species in 83 genera indicates that pubic nipples are absent in megachiropterans and in the majority of microchiropteran families. Pubic nipples appear to be present in all species belonging to the families Rhinopomatidae, Craseonycteridae, Megadermatidae, and Rhinolophidae (including Hipposiderinae). Contrary to previous reports, pubic nipples do not occur in Nycteridae, Emballonuridae, Phyllostomidae, or "nyctophiline" vespertilionids. When present, pubic nipples are ubiquitous in females but may be absent in some males. Although many previous authors have indicated that pubic nipples do not function at all in lactation, gross morphology of pubic nipples suggests that they may have at least some lacteal function in many species. Lactation aside, it is clear that pubic nipples provide important holdfasts for the young in all taxa.

Phylogenetic interpretation of pubic nipples is hampered by uncertainty concerning relationships of bats to other mammalian orders. Based on a variety of evidence, including the absence of pubic nipples in Megachiroptera, it seems most likely that absence of pubic nipples is the primitive condition for bats. Because pubic nipples are present in some families but absent in others, the pattern of taxonomic distribution may contribute to our understanding of higher-level relationships among microchiropteran bats. Interestingly, the distribution of pubic nipples is congruent with immunological distance data and the distribution of derived traits in other anatomical systems (e.g., hyoid musculature, postcranial osteology). However, more work is necessary before these data can be productively analyzed in a comprehensive phylogenetic analysis.

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INTRODUCTION

Most female bats have only one pair of mammae that are located somewhere in the thoracic region, usually in a pectoral or axillary position. This arrangement, seen in both megachiropterans and microchiropterans, is associated with a reproductive pattern that involves producing litters of only one or sometimes two offspring (Tuttle and Stevenson, 1982). In some bats, however, an extra pair of nipples develops in the pubic region just anterior to the vagina. These abdominal nipples are generally called "pubic" nipples (rather than inguinal or preinguinal) because of their close association with the pubic eminence. The function of pubic nipples has been long debated. Some authors refer to them as "organes de fixation" (Rollinat and Trouessart, 1895), "false teats" (Brosset, 1962a, b, c, d, 1963), or "fastening teats" (Kingdon, 1974), suggesting that they function solely or primarily as a holdfast for the young. Other authors have indicated a lacteal function in at least some taxa (Bronn, 1900; Ryberg, 1947; Gaur and Shahrokh, 1989).

The taxonomic distribution of pubic nipples has been discussed by only a few authors. The first explicit statement of taxonomic distribution was that of Ryberg (1947: 155), who reported that "Among bats pubic nipples are found in the families Rhinopomatidae, Megadermatidae, Nycteridae, Rhinolophidae, Hipposideridae, Phyllostomatidae (?), and the subfamily Nyctophilinae." Unfortunately Ryberg (1947) did not discuss the distribution of pubic nipples within these groups, and it is not clear if they are present in all or only some species. The source of Ryberg's distributional data is also unclear; no explicit mention was made of examining specimens, but several comments indicate that Ryberg had firsthand knowledge of pubic nipples in at least some species. Extensive citation of earlier literature on rhinopomatids, rhinolophines, and hipposiderines (e.g., Temminck, 1841; Kolenati, 1857; Anderson and de Winton, 1902; Allen et al., 1917) suggests that much of Ryberg's data came from these early descriptions. The questionable occurrence of pubic nipples in phyllostomids was not discussed further by Ryberg (1947), and there was no mention of his sources of

data on phyllostomids, megadermatids, nycterids, or nyctophiline vespertilionids.

A number of authors have described pubic nipples in the course of taxonomic or reproductive studies. Verschuren (1957) discussed ecology and reproductive biology of 38 bat species from the Belgian Congo. He carefully noted the presence of pubic nipples in each of the rhinolophine, hipposiderine, and megadermatid species but not in any of the six nycterids in the fauna (Verschuren, 1957). Brosset (1962a, b, c, d, 1963) similarly described reproductive habits and mammae of rhinopomatids, megadermatids, rhinolophines, and hipposiderines from central and western India, and noted the presence of pubic nipples in all species referred to these taxa. Rosevear (1965) monographed the bats of west Africa, including rhinopomatids, nycterids, megadermatids, rhinolophines, and hipposiderines, and suggested that pubic nipples are present in all of these families except Rhinopomatidae.

Quay (1970) discussed pubic nipples in a review of the integument of bats, apparently using Ryberg (1947) as the primary source of distributional information on pubic nipples. Hill (1974) added Craseonycteridae to the list of families known to have pubic nipples. Citing Quay (1970) as the source of comparative data, Hill (1974) reported that pubic nipples are present in rhinopomatids, craseonycterids, nycterids, megadermatids, rhinolophids, hipposiderids, nyctophiline vespertilionids, and possibly phyllostomids. The remaining microchiropteran families were listed as lacking pubic nipples in Hill's (1974) tabular summary of character variation. Racey (1988) reported a similar distribution for pubic nipples in an article on assessment of reproductive states in bats, citing Hill (1974) and Quay (1970) as references along with three descriptive papers on African bats (Matthews, 1937a, 1942; Rosevear, 1965). Most recently, Gaur and Shahrokh (1989) indicated that pubic nipples are present in *Rhinopoma microphyllum* and *Taphozous perforatus*, the latter observation representing the first mention of pubic nipples in an emballonurid.

It is clear that one of the problems associated with interpreting chiropteran pubic

nipples is lack of detailed information on taxonomic distribution. Most modern accounts of pubic nipple distribution are ultimately based on the work of Ryberg (1947), who reviewed the earlier literature but did not specify the sources of many of his data. Ryberg's (1947) references to pubic nipples in nycterids, nyctophiline vespertilionids, and possibly phyllostomids are particularly tantalizing because these observations do not appear to have been confirmed by other authors. Similarly, Gaur and Shahrokh's (1989) suggestion of pubic nipples in an emballonurid raises interesting questions since no other authors have reported pubic nipples in this family. Accounts of pubic nipples abound in the literature on rhinopomatids and rhinolophids (e.g., Temminck, 1841; Kolenati, 1857; Anderson and de Winton, 1902; Allen et al., 1917; Matthews, 1937b, 1942; Verschuren, 1957; Brosset, 1962a, b, d, 1963; Rosevear, 1965; Kingdon, 1974) but little has been reported concerning pubic nipples in other taxa.

Morphology of pubic nipples has likewise received little attention. Ryberg (1947: 155, 157) described pubic nipples as follows:

They are seated in the pubic region, close to each other, just anterior to the often transversely lying vulva. They are tube-like appendages with divergent tips, and as a rule are more or less rudimentary. . . . Only in one species, *Hipposideros speoris* Schneider 1826, have they been found . . . to stand in communication with lacteal glands. . . . The pubic nipples may vary widely in size in different species of the same genus, a fact that has been observed both in *Rhinolophus* Lacépède 1799 and *Hipposideros* Gray 1833.

Because no comparative work on pubic nipples has been published, interspecific and interfamilial differences in pubic nipple morphology have yet to be adequately documented. Another unexplored topic involves sexual dimorphism: pubic nipples have been documented in males of some species of *Hipposideros* (Allen et al., 1917), but were reported to be absent in males of *Rhinolophus* and *Megaderma* (Maisonnette, 1878). No data are available on males of other taxa in which females are reported to have pubic nipples.

Because much of the information available

on pubic nipples is anecdotal and/or incomplete, the current study was undertaken with four goals: (1) to survey the taxonomic distribution of pubic nipples in bats; (2) to describe the gross morphology of these nipples in different taxa and sexes; (3) to review the evidence concerning function of pubic nipples in various taxa; and (4) to evaluate the evidence concerning homology and possible phylogenetic significance of pubic nipples in bats.

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ABBREVIATIONS

The following institutional abbreviations are used in this paper: AMNH, American Museum of Natural History, New York; BMNH, British Museum (Natural History), London; TNRC, Thai National Reference Collection, Thailand Institute of Scientific and Technological Research, Bangkok; UMMZ, University of Michigan Museum of Zoology, Ann Arbor, Michigan; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

METHODS

Fluid-preserved specimens of 1164 female and 559 male bats representing 206 species were examined for the presence of pubic nipples (see Appendix). I examined each specimen under a dissecting microscope ($\times 6$ – $\times 40$ magnification) and used canned air (e.g., Beseler Dust Gun) to dry and separate the fur in order to check for vestigial or poorly developed nipples. Parous females were distinguished from nulliparous females based on morphology of the thoracic nipples; see Racey (1988) for a discussion of the use of nipple morphology in reproductive assessment. Relative ages of parous females were estimated based on tooth wear. Lactating females were recognized based on presence of enlarged thoracic nipples, enlarged thoracic mammary glands, and in some instances by association with nursing young (collected with the mother). Because pubic nipples are often hard to detect in males and nulliparous females, I concluded that pubic nipples were absent in a species only when parous females with well-developed thoracic nipples were available for examination.

Measurements of pubic nipples in parous females were made using dial calipers, and morphological variations were noted where appropriate. I examined internal morphology of pubic nipples and degree of development of subcutaneous mammary glands through dissections of selected specimens. Lacteal tissue was recognized by its texture, color, and relationships to both the nipple and to the facial layers of the anterior body wall. Histology of pubic nipples was not investigated in the current study.

The phylogenetic significance of pubic nipples was evaluated by mapping the taxonomic distribution of pubic nipples on alternative phylogenetic trees. MacClade version 3.0 (Maddison and Maddison, 1992) was used to investigate possible patterns of character transformation and to produce the illustrations presented in figures 8–12.

MORPHOLOGY AND TAXONOMIC DISTRIBUTION OF PUBIC NIPPLES IN BATS

RHINOPOMATIDAE

This small family of Old World bats comprises three species (Koopman, 1993), all of

which have pubic nipples (table 1). Nulliparous females have tiny pubic nipples that are similar in form to the undeveloped thoracic nipples. Pubic nipples in nulliparous *Rhinopoma hardwickei* and *R. microphyllum* appear as dense, light-colored lumps in the skin; in *R. muscatellum* they are the same color as the surrounding skin and are distinguished principally by contour and texture. Parous females that exhibit well-developed, pendant thoracic nipples have pubic nipples that are approximately the same size as the thoracic nipples. Pubic nipples of parous females are elongate, paddle-shaped structures that are generally somewhat flattened (fig. 1; see table 2 for measurements). In many individuals the base of the nipple is constricted to form a pedicle that supports the broader distal portion of the nipple. In older individuals (fig. 1B) the pedicle may become quite long, and the nipple may be recurved distally. This morphology is associated with development of a tough, keratinous sheath on the posterior and lateral surfaces of the pubic nipples. The sheath is most obvious at the distal end of the nipple, where it may become thickened and overhang the nipple tip (fig. 1B, right nipple). Openings can be detected in the tips of pubic nipples in some specimens, including all lactating individuals examined (e.g., AMNH 208126 [*Rhinopoma hardwickei*]; USNM 336331 [*R. microphyllum*]). Right and left pubic nipples are approximately the same size at all ages. Pigmentation of pubic nipples is light in all species, matching that of the abdominal skin.

Pubic nipples of female rhinopomatids appear to be functional in lactation. Gaur and Shahrokh (1989) observed and photographed what they interpreted as young *Rhinopoma microphyllum* sucking milk from pubic nipples, an observation supported by anatomical evidence. Anderson and de Winton (1902) described the internal structure of pubic nipples in *Rhinopoma* and noted that these nipples contain a single main duct into which several secondary ducts open. All the ducts appear lined with epithelium, and the main duct opens externally at the distal tip of the nipple (Anderson and de Winton, 1902). My dissections of fluid-preserved lactating females of *Rhinopoma hardwickei* (e.g., AMNH 208126) revealed presumptive lacteal tissue associated with the pubic nipples, although

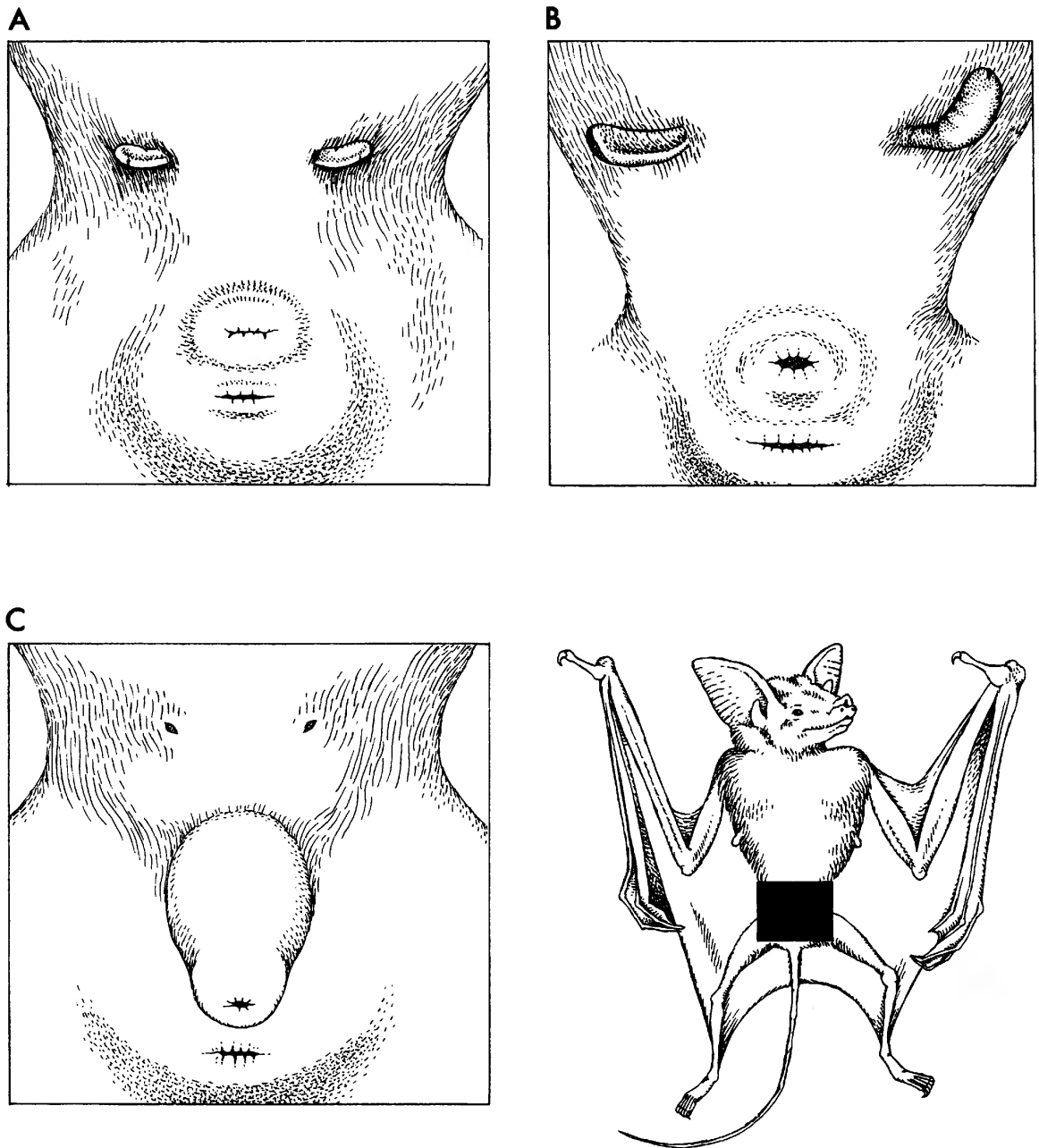


Fig. 1. Close-up views of the genital region showing pubic nipples in female and male rhinopomatids. **A.** Young parous female *Rhinopoma hardwickei* (AMNH 208125). **B.** Old parous female *Rhinopoma microphyllum* (AMNH 212070). The right nipple of the bat has been slightly twisted to expose the anterior surface of the nipple; the left nipple is positioned to show the posterior surface. Note the keratinous sheath visible on the tip of the right nipple. In older female rhinopomatids this sheath typically covers the posterior and lateral surfaces of the nipple (largely hidden from view in this figure) and extends distally somewhat beyond the tip of the nipple. The sheath on the left nipple was removed to facilitate examination of the underlying tissues. **C.** Adult male *Rhinopoma microphyllum* (AMNH 236214). The pubic nipples appear as a pair of tiny lumps in the skin anterior to the penis. The degree of pubic nipple development seen in this male is similar to that of nulliparous females.

TABLE 1
Occurrence of Pubic Nipples in Rhinopomatidae, Craseonycteridae, and Megadermatidae^a

Taxon	Females	Males
Rhinopomatidae		
<i>Rhinopoma hardwickei</i>	present (17)	present (12) absent (4)
<i>Rhinopoma microphyllum</i>	present (8)	present (12) absent (2)
<i>Rhinopoma muscatellum</i>	present (10)	present (4) absent (3)
Craseonycteridae		
<i>Craseonycteris thonglongyai</i>	present (1)	present (2)
Megadermatidae		
<i>Megaderma lyra</i>	present (6)	present (9)
<i>Megaderma spasma</i>	present (13)	present (5)
<i>Macroderma gigas</i>	present (8)	?
<i>Lavia frons</i>	present (14)	present (9)
<i>Cradioderma cor</i>	present (13)	present (11)

^a Pubic nipples were scored as "present" when they could be unambiguously identified using a dissecting microscope ($\times 6$ – $\times 40$ magnification); nipples were scored as "absent" only when no trace of pubic nipples could be found upon examination of well-preserved specimens. The number of individuals exhibiting each condition is given in parentheses. "?" indicates that no appropriately preserved specimens were available for the taxon and sex indicated. No histological techniques were employed to obtain these data; all observations were based on gross morphology of fluid-preserved museum specimens. See Appendix for a list of the specimens examined.

it is much less extensive than the grossly similar glandular tissue associated with the thoracic nipples. On this basis it seems likely that pubic nipples of rhinopomatids provide young bats with at least some milk.

Small pubic nipples are variably present in male rhinopomatids (table 1). Pubic nipples occur in the majority of individuals, but they are entirely lacking in at least some specimens of each species. Male pubic nipples resemble the nipples of nulliparous females, generally appearing as tiny oval bumps or ridges in the abdominal skin (fig. 1C). In one old male *Rhinopoma microphyllum kinneari* (AMNH 236214) the pubic nipples are spotted with dark pigment, but the majority of male nipples are the same color as the surrounding skin.

CRASEONYCTERIDAE

This monotypic family includes only *Craseonycteris thonglongyai* from Thailand (Koopman, 1993). Hill (1974: 309) reported the presence of pubic nipples in his original description of this species, describing them as "closely set and situated just anterior to the genital eminence." No mention was made of occurrence of pubic nipples in male individuals.

Three adult *Craseonycteris* (1 female and 2 males) were available for the current study (see Appendix). The female (BMNH 77.3009), a parous individual with well-developed thoracic nipples, has very long tubular pubic nipples that are lightly pigmented and do not have a keratinous sheath. Although an opening is clearly visible in the tip of each thoracic nipple, there is no evidence of an opening or perforation in the tip of the pubic nipples.

The pubic nipples in the preserved specimen described above closely resemble those illustrated in an excellent color photograph of a lactating female taken by S. Duangkhae (fig. 2; reproduced from Duangkhae, 1990). The thoracic nipples in this individual are swollen with milk; they appear almost white, corresponding in color to the surrounding hairless skin over the mammary glands. In contrast, the pubic nipples are dark red and appear to contain no milk. Unfortunately, I could not confirm absence of lacteal tissue in the pubic region of *Craseonycteris* because no lactating individuals were available for dissection.

Both of the male *Craseonycteris* that I examined exhibit vestigial pubic nipples. These nipples appear as tiny, light-colored lumps in the skin anterior to the penis.



Fig. 2. Photograph by Surapon Duangkhae showing a lactating female *Craseonycteris thonglongyai* with well-developed pubic nipples (reproduced from Duangkhae, 1990). Note the differences in shape and color between the pubic and the thoracic nipples.

EMBALLONURIDAE

This tropical family includes 13 genera and 46 species (Koopman, 1993). The only report of pubic nipples in an emballonurid is that of Gaur and Shahrokh (1989), who indicated that *Taphozous perforatus* has both thoracic and pubic nipples. However, my examination of 23 fluid-preserved females of this species (including 11 parous individuals with well-developed thoracic nipples) failed to reveal a single animal with pubic nipples. Examination of females representing 20 additional emballonurid species similarly revealed no pubic nipples (see Appendix). On the basis of these observations it seems unlikely that any emballonurid species has pubic nipples.

NYCTERIDAE

This Old World family comprises a single genus (*Nycteris*) with 12 species (Koopman, 1993). Despite Ryberg's (1947) statement that nycterids have pubic nipples, my examina-

tion of 116 females representing 10 species failed to reveal a single individual with pubic nipples (see Appendix). A review of the literature reveals that neither Ryberg (1947)—nor any of the publications cited by him—explicitly described pubic nipples in a nycterid. Quay (1970), Hill (1974), Van Valen (1979), and Racey (1988)—all of whom list nycterids as having pubic nipples—appear to have relied on Ryberg (1947) as the source of their information; these publications neither documented occurrence of pubic nipples in nycterids nor cited any additional evidence supporting this hypothesis. As mentioned previously, Verschuren (1957) noted the presence of pubic nipples in rhinolophids and megadermatids from the Belgian Congo, but he did not report pubic nipples in any of the six nycterids in the fauna. Rosevear (1965) described pubic nipples in west African megadermatids and rhinolophids, but pubic nipples were not explicitly described in nycterids despite a claim in the introduction. Given the absence of a single documented

TABLE 2
Variation in Size of Pubic Nipples of Parous
Female Rhinopomatids, Craseonycterids, and
Megadermatids

Taxon	N ^a	Length ^b	
		Range	Mean
Rhinopomatidae			
<i>Rhinopoma hardwickei</i>	6	1.9–2.3	2.0
<i>Rhinopoma microphyllum</i>	6	2.4–3.5	2.8
<i>Rhinopoma muscatellum</i>	4	1.7–2.4	2.0
Craseonycteridae			
<i>Craseonycteris thonglongyai</i>	1	2.7	2.7
Megadermatidae			
<i>Megaderma lyra</i>	1	3.9	3.9
<i>Megaderma spasma</i>	9	1.9–5.3	3.3
<i>Macroderma gigas</i>	5	4.0–7.0	5.2
<i>Lavia frons</i>	10	1.2–4.4	2.7
<i>Cardiaderma cor</i>	11	1.5–6.6	3.6

^a N is the number of individuals measured (the number of nipples = 2N). Left and right pubic nipples were equal in length in each of the individuals examined.

^b Nipple length was measured from the ventral body wall to the tip of the nipple; measurements are given in millimeters and were recorded to 0.1 mm. See Appendix for a list of the specimens measured.

occurrence, it now seems likely that pubic nipples are absent in Nycteridae.

MEGADERMATIDAE

This Old World family includes five extant species referred to four genera (Koopman, 1993). Females of all species have pubic nipples that are typically similar in size to the thoracic nipples (table 1). Nulliparous females exhibit tiny pubic nipples that appear only as lumps in the skin. When well-developed, pubic nipples of megadermatids have the appearance of elongate, flattened tubes with little or no pedicle and no evidence of any perforations or openings (fig. 3A). The size of pubic nipples appears to increase over time; older individuals (as judged by tooth wear) usually have longer pubic nipples than younger individuals. Right and left pubic nipples are equivalent in size at all ages. In older individuals, the distal tip of the nipple typically becomes somewhat expanded laterally, and the posterior and lateral surfaces develop a tough, keratinous sheath that may overhang

the tip of the nipple (fig. 3B). This morphology closely resembles that seen in older rhinopomatids (e.g., fig. 1B).

A single parous individual of *Macroderma gigas* (USNM 578488) was found to have an extra pubic nipple on the left side. In this specimen, two symmetrically placed “normal” pubic nipples (each 4.0 mm in length) are located in the usual positions anterior and lateral to the labia. The extra nipple, which is conical and projects approximately 1.0 mm from the body wall, is located midway between the left pubic nipple and the labia. This is the only example of a supernumerary pubic nipple found among the 636 female bats bearing pubic nipples examined in this study.

In *Megaderma*, *Macroderma*, and *Cardiaderma*, the pubic nipples of all females are pale, matching the color of the surrounding skin. The keratinous sheath seen in older females is brown but somewhat transparent; the light color of the nipple can always be distinguished, particularly on the anterior surface of the nipple (which typically lacks the keratinous layer). In *Lavia*, however, all surfaces of the pubic nipples are heavily pigmented, appearing almost black in parous females. This matches the pigmentation of the thoracic nipples. In nulliparous *Lavia* pigmentation is less noticeable but still present, usually appearing as a dark ring around the tiny nipple.

Dissections of lactating female *Megaderma spasma* (AMNH 247230) and *Macroderma gigas* (fig. 3B; AMNH 236544) failed to reveal any lacteal tissue associated with the pubic nipples. Taken together with the absence of discernible openings in the pubic nipples, these observations suggest that pubic nipples do not function in lactation in Megadermatidae.

All adult male megadermatids examined in this study exhibited small pubic nipples located just anterior and lateral to the penis (table 1; fig. 3C). Male pubic nipples are about the same size as those of nulliparous females, comprising a simple lump in the skin. In some males (e.g., *Megaderma spasma*, AMNH 225449) the nipples are slightly larger, projecting up to 0.8 mm from the surrounding skin. Well-developed male nipples like these are usually folded over and appear as tiny flaps in fluid-preserved specimens (fig. 3C). Pubic nipples in older males are covered by

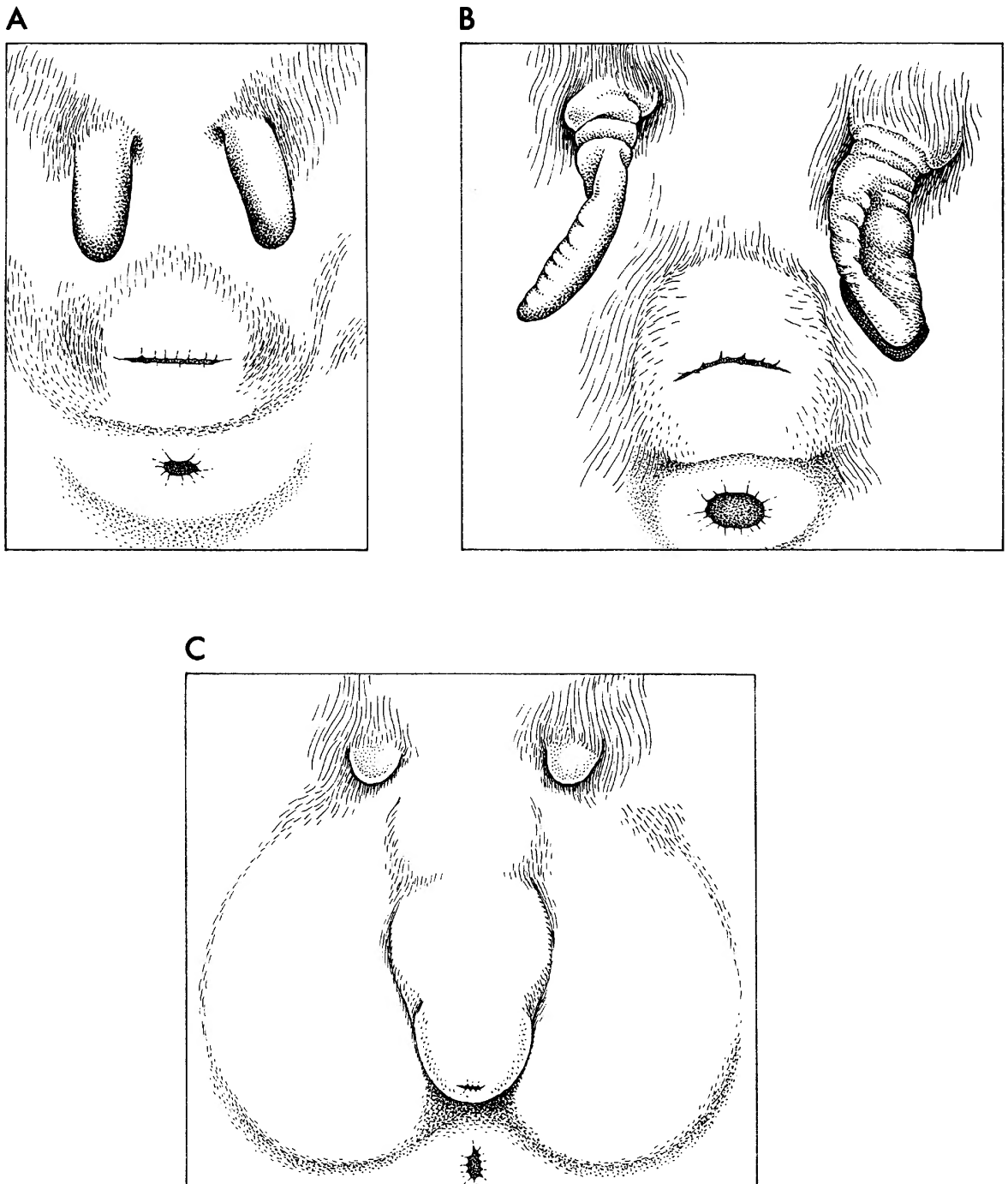


Fig. 3. Pubic nipples in female and male megadermatids. **A.** Parous female *Megaderma spasma* (AMNH 225547). **B.** Old lactating female *Macroderma gigas* (AMNH 236544). The right nipple of the bat is twisted to provide a medial view of the nipple; the left nipple has been positioned to show the anterior surface. A keratinous sheath is visible on the tip of the left nipple. The sheath on the right nipple was removed to facilitate examination of the underlying tissues. There is no evidence of a duct system or openings in the tips of either nipple. This individual is known to have been lactating at the time of collection because she was carrying a small juvenile offspring (AMNH 236545). **C.** Adult male *Megaderma spasma* (AMNH 225449). Although not visible in this illustration, the nipples are covered with a transparent keratinous covering similar to that seen on the pubic nipples of older females.

TABLE 3
Occurrence of Pubic Nipples in Selected Rhinolophine Rhinolophids

Taxon ^a	Females	Males
Rhinolophinae		
<i>Rhinolophus</i>		
<i>euryotis</i> group		
<i>Rhinolophus arcuatus</i>	present (8)	present (7)
<i>Rhinolophus canuti</i>	present (8)	present (3) absent (5)
<i>Rhinolophus coelophyllus</i>	present (3)	present (7)
<i>Rhinolophus creaghi</i>	present (2)	?
<i>Rhinolophus euryotis</i>	present (6)	present (9)
<i>Rhinolophus inops</i>	present (11)	present (3) absent (1)
<i>Rhinolophus rufus</i>	present (2)	present (5)
<i>Rhinolophus shameli</i>	?	present (4)
<i>ferrumequinum</i> group		
<i>Rhinolophus affinis</i>	present (14)	present (6) absent (2)
<i>Rhinolophus borneensis</i>	present (11)	present (9)
<i>Rhinolophus clivosus</i>	present (2)	present (20)
<i>Rhinolophus darlingi</i>	present (8)	present (4) absent (1)
<i>Rhinolophus deckenii</i>	present (4)	present (1)
<i>Rhinolophus denti</i>	?	present (1)
<i>Rhinolophus ferrumequinum</i>	present (3)	present (1)
<i>Rhinolophus malayanus</i>	present (1)	present (3)
<i>Rhinolophus megaphyllus</i>	present (27)	present (17) absent (1)
<i>Rhinolophus robinsoni</i>	?	present (1)
<i>Rhinolophus rouxi</i>	present (34)	present (5)
<i>Rhinolophus simplex</i>	present (2)	present (1)
<i>Rhinolophus simulator</i>	present (1)	?
<i>Rhinolophus stheno</i>	present (9)	present (6)
<i>Rhinolophus thomasi</i>	present (5)	present (1)
<i>Rhinolophus virgo</i>	present (3)	present (11)
<i>hipposideros</i> group		
<i>Rhinolophus hipposideros</i>	present (4)	present (6)
<i>luctus</i> group		
<i>Rhinolophus eloquens</i>	present (6)	present (6)
<i>Rhinolophus fumigatus</i>	present (9)	present (16)
<i>Rhinolophus hildebrandti</i>	present (1)	present (9)
<i>Rhinolophus luctus</i>	present (9)	present (7)
<i>Rhinolophus macrotis</i>	present (2)	present (7) absent (1)
<i>Rhinolophus pearsoni</i>	present (5)	present (3)
<i>Rhinolophus philippinensis</i>	present (2)	present (5)
<i>Rhinolophus rex</i>	present (1)	present (1)
<i>Rhinolophus sedulus</i>	present (3)	present (3)
<i>Rhinolophus trifoliatus</i>	present (6)	present (4)
<i>pusillus</i> group		
<i>Rhinolophus acuminatus</i>	present (5)	present (3)
<i>Rhinolophus alcyone</i>	present (3)	present (1)
<i>Rhinolophus blasii</i>	present (2)	present (2)
<i>Rhinolophus cornutus</i>	present (20)	present (3) absent (5)
<i>Rhinolophus euryale</i>	present (12)	present (14)
<i>Rhinolophus guineensis</i>	present (1)	present (1)
<i>Rhinolophus imaizumii</i>	?	present (4) absent (3)
<i>Rhinolophus landeri</i>	present (2)	present (3)
<i>Rhinolophus lepidus</i>	present (24)	present (29) absent (2)

TABLE 3—(Continued)

Taxon ^a	Females	Males
<i>Rhinolophus mehelyi</i>	present (16)	present (3)
<i>Rhinolophus monoceros</i>	present (3)	present (2) absent (9)
<i>Rhinolophus osgoodi</i>	present (21)	present (3)
<i>Rhinolophus pusillus</i>	present (16)	present (6) absent (6)

^a The classification presented here is that of Koopman (in press). See Appendix for a list of the specimens examined.

a keratinous layer similar to that described above for older females; in this way they differ from nulliparous females, which never exhibit such a covering. Although no fluid-preserved male *Macroderma gigas* were available for study, it seems likely that all adult male megadermatids have pubic nipples.

RHINOLOPHIDAE: RHINOLOPHINAE

The family Rhinolophidae currently comprises two Old-World subfamilies, Rhinolophinae and Hipposiderinae; Rhinolophinae contains one extant genus (*Rhinolophus*) with 64 species (Koopman, 1993). Examination of fluid-preserved specimens representing 48 species suggests that all rhinolophine species probably possess pubic nipples (table 3). All of the 337 females that I examined had pubic nipples, but this was not true of the males. As in rhinopomatids, pubic nipples were found in males of each rhinolophine species examined, but not in every male individual. Within-species polymorphism (i.e., pubic nipples variably present or absent in males) was observed in 11 species, 23% of the rhinolophine species considered in this study.

Morphology of female pubic nipples shows a regular pattern of ontogenetic variation throughout Rhinolophinae. Nulliparous females are characterized by pubic nipples that appear as small oval lumps or transverse ridges that are situated with the long axis oriented roughly mediolaterally. In parous females the pubic nipples tend to retain the same form at the base; they are elongate mediolaterally but anteroposteriorly compressed. Young parous females with only moderate nipple development have pubic nipples which are wider than they are long; these appear as flaps in fluid-preserved spec-

imens. In older females the nipples eventually elongate and may become somewhat wider distally, giving the nipple a paddlelike appearance similar to that seen in rhinopomatids and megadermatids.

The majority of specimens examined exhibit right and left nipples of equivalent size (table 4). In five individuals, however, one pubic nipple is markedly larger than the other. This was seen in *Rhinolophus euryotis* (AMNH 158464; left nipple 1.7 mm long, right 0.7 mm), *R. lepidus* (AMNH 234076; left 1.9 mm, right 0.9 mm), *R. rufus* (USNM 459502; left 3.0 mm, right 2.5 mm), *R. sedulus* (AMNH 234089; left 2.5, right 1.8), and *R. steno* (AMNH 232527; left 1.7, right 0.5). These appear to be unusual occurrences even within the species in question. In *R. lepidus*, for example, only one out of the 13 parous females examined has asymmetrical development of the pubic nipples. Nipple asymmetry appears to be correlated with age (or number of pregnancies); all of the individuals noted above are relatively old females that exhibit some of the largest pubic nipples recorded for their species.

My dissections of the few lactating females available indicate that lacteal tissue is associated with the pubic nipples in at least some rhinolophine species. All of the lactating individuals dissected (e.g., *Rhinolophus cornutus* [AMNH 215772]; *R. luctus* [AMNH 45123, 247310]; *R. sedulus* [AMNH 234090]; *R. trifolius* [USNM 152090]) exhibit some development of lacteal tissue at the base of the pubic nipples. In these individuals the pubic nipples are plump with perforated tips. Pressure applied to these nipples generally results in expulsion of fluid through the openings. Apical perforations are also present in the plump pubic nipples of some parous specimens of *R. hildebrandti* (AMNH 216207), *R. hipposideros* (USNM 476921), *R. macrotis*

TABLE 4
Proportions of Pubic Nipples in Parous Female Rhinolophine Rhinolophids

Taxon ^a	N ^b	Length ^c		Nipple asymmetry ^d			Mean difference in length
		Range	Mean	L > R	L = R	L < R	
Rhinolophinae							
<i>Rhinolophus</i>							
<i>euryotis</i> group							
<i>Rhinolophus arcuatus</i>	3	0.9–1.3	1.1	0	3	0	—
<i>Rhinolophus coelophyllus</i>	2	0.5–1.0	0.8	0	2	0	—
<i>Rhinolophus creaghi</i>	1	1.2	1.2	0	1	0	—
<i>Rhinolophus euryotis</i>	4	0.7–1.7	1.4	0	3	1	0.3
<i>Rhinolophus inops</i>	7	1.0–1.4	1.2	0	7	0	—
<i>Rhinolophus rufus</i>	2	2.5–3.0	2.7	1	1	0	0.2
<i>ferrumequinum</i> group							
<i>Rhinolophus affinis</i>	10	0.6–2.0	1.2	0	10	0	—
<i>Rhinolophus borneensis</i>	10	1.0–1.6	1.4	0	10	0	—
<i>Rhinolophus clivus</i>	2	1.5–1.9	1.7	0	2	0	—
<i>Rhinolophus darlingi</i>	5	1.4–3.0	2.6	0	5	0	—
<i>Rhinolophus deckenii</i>	4	1.4–2.6	2.0	0	4	0	—
<i>Rhinolophus ferrumequinum</i>	3	2.3–3.3	2.9	0	3	0	—
<i>Rhinolophus malayanus</i>	1	1.7	1.7	0	1	0	—
<i>Rhinolophus megaphyllus</i>	15	0.9–3.0	1.8	0	15	0	—
<i>Rhinolophus rouxi</i>	11	0.5–2.5	1.8	0	11	0	—
<i>Rhinolophus simplex</i>	1	0.7	0.7	0	1	0	—
<i>Rhinolophus simulator</i>	1	1.2	1.2	0	1	0	—
<i>Rhinolophus stheno</i>	5	0.5–1.7	0.9	1	4	0	0.2
<i>Rhinolophus thomasi</i>	3	1.1–1.9	1.5	0	3	0	—
<i>Rhinolophus virgo</i>	3	0.9–1.2	1.0	0	3	0	—
<i>hipposideros</i> group							
<i>Rhinolophus hipposideros</i>	2	0.7–1.6	1.2	0	2	0	—
<i>luctus</i> group							
<i>Rhinolophus eloquens</i>	4	1.4–2.8	1.9	0	4	0	—
<i>Rhinolophus hildebrandti</i>	1	2.9	2.9	0	1	0	—
<i>Rhinolophus luctus</i>	7	1.2–5.2	2.8	0	7	0	—
<i>Rhinolophus macrotis</i>	2	1.5–1.7	1.6	0	2	0	—
<i>Rhinolophus pearsoni</i>	3	1.8–2.0	1.9	0	3	0	—
<i>Rhinolophus philippinensis</i>	2	0.9–2.4	2.1	0	2	0	—
<i>Rhinolophus sedulus</i>	2	1.2–2.5	1.7	1	1	0	0.4
<i>Rhinolophus trifoliatus</i>	5	0.9–4.1	2.8	0	5	0	—
<i>pusillus</i> group							
<i>Rhinolophus acuminatus</i>	3	1.0–1.5	1.3	0	3	0	—
<i>Rhinolophus alcyone</i>	2	1.5–2.2	1.9	0	2	0	—
<i>Rhinolophus blasii</i>	2	0.8–1.5	1.2	0	2	0	—
<i>Rhinolophus cornutus</i>	17	0.6–2.2	1.0	0	17	0	—
<i>Rhinolophus euryale</i>	2	2.1–2.3	2.2	0	2	0	—
<i>Rhinolophus guineensis</i>	1	1.6	1.6	0	1	0	—
<i>Rhinolophus landeri</i>	1	2.0	2.0	0	1	0	—
<i>Rhinolophus lepidus</i>	13	0.9–2.0	1.4	1	12	0	0.1
<i>Rhinolophus mehelyi</i>	9	1.6–2.5	2.1	0	9	0	—

TABLE 4—(Continued)

Taxon ^a	N ^b	Length ^c		Nipple asymmetry ^d			Mean difference in length
		Range	Mean	L > R	L = R	L < R	
<i>Rhinolophus osgoodi</i>	5	0.6–1.2	1.0	0	5	0	—
<i>Rhinolophus pusillus</i>	8	0.7–1.8	1.1	0	8	0	—

^a The classification presented here is that of Koopman (in press).

^b N is the number of individuals measured (the number of nipples = 2N). See Appendix for a list of the specimens measured.

^c Nipple length was measured from the ventral body wall to the tip of the nipple; measurements are given in millimeters and were recorded to 0.1 mm.

^d L refers to the left pubic nipple and R refers to the right pubic nipple of a single individual. "L > R" indicates the number of individuals in which the left nipple is longer than the right; "L = R" indicates the number of individuals in which the nipples are subequal; and "L < R" indicates cases in which the right nipple is longer than the left. Mean difference in length between the right and left nipples was calculated for N parous individuals.

(AMNH 234057), *R. megaphyllus* (e.g., AMNH 158475, 220076), *R. mehelyi* (e.g., USNM 476859, 475860), *R. pearsoni* (USNM 102464), and *R. rouxi* (AMNH 48011). Many of these specimens were either pregnant or lactating at the time of preservation. Most nonlactating parous females have flaccid and apparently imperforate pubic nipples.

A keratinous sheath is present on the posterior and lateral surfaces of the nipple of some parous female *Rhinolophus alcyone* (USNM 546972), *R. deckeni* (AMNH 208341), *R. luctus* (AMNH 247276), and *R. trifolius* (USNM 153961). As in rhinopomatids and megadermatids, this covering appears only in older females. Interestingly, the keratinous sheath is absent in older females of *R. luctus* and *R. trifolius* that were lactating at the time of preservation, suggesting that the layer may be lost each time lactation occurs. A possible scenario is that the sheath is lost when the pubic nipples swell and a young bat begins nursing, and then develops anew after lactation ceases if the young bat continues to attach itself to the mother using the pubic nipples. Lack of a keratinous sheath in the majority of the specimens observed may be in part an effect of sampling and preservation: older females are not available for all taxa, and the sheath is easily dislodged when specimens are handled. Nevertheless, the pattern in rhinolophines appears different from that seen in megadermatids and hipposiderines, in which virtually all of the older

females have a keratinous sheath on their pubic nipples.

The majority of rhinolophine species have pubic and thoracic nipples that either lack distinctive pigmentation or are lightly pigmented (light brown, darker than the surrounding skin). However, in at least one species the nipples exhibit an unusual pattern of pigmentation: the pubic nipples in *Rhinolophus luctus* are gray-brown with white tips, a pattern that is seen in males as well as females.

Consideration of the rhinolophine specimens examined in this study suggests that the majority of morphological differences in female pubic nipples are a function of (1) age of the individual and the number of offspring nursed; (2) reproductive state at time of death (lactating or nonlactating); and (3) state of preservation of the specimen. The within-species variation observed in the larger series of parous females equals or exceeds differences seen among specimens from different *Rhinolophus* species; the only exception is the pigmentation of the nipples in *R. luctus*, which appears to be autapomorphic. If other significant among-species differences exist, they cannot be identified unambiguously given the material and methods described here. More comprehensive studies involving animals with known reproductive histories (sampled at equivalent reproductive states) will be necessary to determine if additional significant differences exist among rhinolophid species.

TABLE 5
Occurrence of Pubic Nipples in Selected Hipposiderine Rhinolophids

Taxon ^a	Females	Males
Hipposiderinae		
Coelopsini		
<i>Coelops frithi</i>	present (15)	present (10)
Hipposiderini		
Rhinonycterina		
<i>Cloeotis percivali</i>	present (2)	?
<i>Rhinonycteris aurantia</i>	present (1)	present (2)
<i>Triaenops persicus</i>	present (7)	present (9)
Hipposiderina		
<i>Anthops ornatus</i>	?	present (1)
<i>Asellia tridens</i>	present (12)	present (17) absent (2)
<i>Aselliscus</i>		
<i>Aselliscus stoliczkanus</i>	present (5)	present (7) absent (1)
<i>Aselliscus tricuspidatus</i>	present (10)	present (9)
<i>Hipposideros</i>		
armiger group		
<i>Hipposideros armiger</i>	present (6)	present (2)
<i>Hipposideros turpis</i>	present (5)	present (3)
bicolor group		
<i>Hipposideros ater</i>	present (12)	present (8)
<i>Hipposideros beatus</i>	present (1)	present (1)
<i>Hipposideros bicolor</i>	present (3)	present (4)
<i>Hipposideros caffer</i>	present (13)	present (3)
<i>Hipposideros calcaratus</i>	present (1)	present (2)
<i>Hipposideros cineraceus</i>	present (6)	present (1)
<i>Hipposideros dyacorum</i>	present (6)	present (1)
<i>Hipposideros fuliginosus</i>	present (5)	?
<i>Hipposideros fulvus</i>	present (3)	present (3)
<i>Hipposideros galeritus</i>	present (3)	present (1)
<i>Hipposideros jonesi</i>	present (8)	present (2)
<i>Hipposideros lamottei</i>	present (1)	present (1)
<i>Hipposideros maggietaylorae</i>	present (6)	present (3)
<i>Hipposideros obscurus</i>	present (4)	present (6)
<i>Hipposideros papua</i>	present (1)	?
<i>Hipposideros pygmaeus</i>	present (5)	present (5)
<i>Hipposideros ridleyi</i>	present (1)	present (1)
<i>Hipposideros ruber</i>	present (11)	present (14)
<i>Hipposideros sabanus</i>	present (1)	present (1)
cyclops group		
<i>Hipposideros cyclops</i>	present (6)	present (9)
<i>Hipposideros muscinus</i>	present (1)	present (4)
<i>Hipposideros semoni</i>	present (2)	?
<i>Hipposideros stenotis</i>	present (1)	?
diadema group		
<i>Hipposideros commersoni</i>	present (9)	present (12)
<i>Hipposideros diadema</i>	present (16)	present (26)
<i>Hipposideros lankadiva</i>	?	present (1)
megalotis group		
<i>Hipposideros megalotis</i>	present (1)	?
pratti group		
<i>Hipposideros pratti</i>	present (8)	present (3)

TABLE 5—(Continued)

Taxon ^a	Females	Males
<i>speoris</i> group		
<i>Hipposideros larvatus</i>	present (9)	present (7)
<i>Hipposideros speoris</i>	present (2)	present (2)

^a The classification presented here is that of Koopman (in press). See Appendix for a list of the specimens examined.

Pubic nipples occur in males of all of the rhinolophine species examined in this study (table 3). These nipples resemble those of nulliparous females, although in some cases they exhibit less relief (i.e., they may appear as tiny smooth patches on the skin rather than as tiny lumps). There is some within-species variation in the form of male pubic nipples: compared to young males, older males usually exhibit pubic nipples that more closely approximate the degree of development seen in nulliparous females. A keratinous covering of the pubic nipples was detected in the older males of only two species, *Rhinolophus clivosus* and *R. hipposideros*.

Pubic nipples are ubiquitous in males in the majority of species, but a few male individuals lack any trace of pubic nipples (table 3). This polymorphism was observed in 11 species: *Rhinolophus affinis*, *R. canuti*, *R. cornutus*, *R. darlingi*, *R. imaizumii*, *R. inops*, *R. lepidus*, *R. macrotis*, *R. megaphyllus*, *R. monoceros*, and *R. pusillus*. When pubic nipples are present in males of these species, they are minute and show little relief. This pattern may represent a condition intermediate between complete absence of pubic nipples and presence of well-developed nipples in all male individuals.

RHINOLOPHIDAE: HIPPOSIDERINAE

This subfamily of rhinolophids contains 66 extant species in 9 genera (Koopman, 1993). My examination of fluid-preserved specimens of 40 species in 8 genera suggests that all hipposiderine species possess pubic nipples (table 5). The morphology of female pubic nipples shows a great deal of variation within species and even within individuals (figs. 4, 5; table 6). Pubic nipples in nulliparous females are similar in all species examined, resembling small lumps or flaps of skin that are approximately as long as they

are wide (fig. 4B). The morphology of pubic nipples in parous hipposiderines differs little from that of rhinolophines. When the pubic nipples are relatively short (e.g., length < 4 × width at base), the nipple appears as a blunt, cylindrical structure (fig. 4C). The distal half of relatively longer nipples is generally laterally expanded, anterodorsally recurved, and covered with a keratinous sheath covering the posterior and lateral surfaces (fig. 4D). Younger females have pubic nipples with the former morphology (blunt, cylindrical), older individuals tend to exhibit the latter morphology, and females with asymmetrical pubic nipples may have one of each type (fig. 5). Pubic nipples of non-lactating parous females generally appear flaccid no matter what their morphology, and perforations or openings are not apparent on the nipple tips.

Lactating females of several species were available for the current study: *Hipposideros bicolor* (USNM 237956), *H. commersoni* (USNM 347412, 347414), *H. diadema* (AMNH 234152), and *H. pygmaeus* (USNM 459443). The specimens of *H. bicolor*, *H. diadema*, and *H. pygmaeus* have plump, cylindrical pubic nipples with a large central duct (visible externally as a longitudinal groove in the surface of the nipple) and perforations in the tip. Dissection of AMNH 234152 (*H. diadema*) revealed the presence of lacteal tissue associated with the nipples. Both individuals of *H. commersoni* are older females with a keratinous sheath on the expanded distal end of the pubic nipples. Perforations are visible in the pubic nipples of USNM 347412 but not USNM 347414; neither specimen was dissected in the current study.

Pigmentation of nipples in hipposiderines appears to increase with age. Pubic nipples of nulliparous females either lack pigment and appear white in fluid-preserved specimens, or are lightly pigmented and appear slightly darker than the surrounding skin. In

TABLE 6
Proportions of Pubic Nipples in Parous Female Hipposiderine Rhinolophids

Taxon ^a	N ^b	Length ^c		Nipple asymmetry ^d			Mean difference in length
		Range	Mean	L > R	L = R	L < R	
Hipposiderinae							
Coelopsini							
<i>Coelops frithi</i>	8	0.8–2.9	1.6	2	2	4	0.7
Hipposiderini							
Rhinonycterina							
<i>Cloeotis percivali</i>	1	1.0	1.0	0	1	0	—
<i>Rhinonycteris aurantia</i>	1	1.2	1.2	0	1	0	—
<i>Triaenops persicus</i>	6	0.8–1.9	1.4	0	6	0	—
Hipposiderina							
<i>Asellia tridens</i>	4	1.7–2.4	2.1	0	4	0	—
<i>Aselliscus</i>							
<i>Aselliscus stoliczkanus</i>	2	0.4–2.5	1.3	1	0	1	1.7
<i>Aselliscus tricuspidatus</i>	7	0.4–3.5	2.0	3	3	1	0.8
<i>Hipposideros</i>							
armiger group							
<i>Hipposideros armiger</i>	4	1.3–5.6	3.0	3	1	0	1.8
<i>Hipposideros turpis</i>	2	1.8–3.9	2.6	1	0	1	1.6
bicolor group							
<i>Hipposideros ater</i>	11	1.6–3.6	2.1	3	5	3	0.8
<i>Hipposideros bicolor</i>	3	1.5–3.3	2.0	1	2	0	0.5
<i>Hipposideros caffer</i>	5	0.9–4.0	1.5	1	2	2	0.9
<i>Hipposideros calcaratus</i>	1	1.4	1.4	0	1	0	—
<i>Hipposideros cineraceus</i>	2	1.5–2.8	2.4	0	1	1	0.5
<i>Hipposideros dyacorum</i>	4	1.3–2.6	2.4	2	1	1	1.1
<i>Hipposideros fuliginosus</i>	4	1.4–4.2	2.3	1	1	2	1.2
<i>Hipposideros fulvus</i>	3	1.0–2.5	1.6	1	2	0	0.1
<i>Hipposideros galeritus</i>	2	1.0–2.6	1.9	1	1	0	0.8
<i>Hipposideros jonesi</i>	3	1.7–3.2	2.3	1	1	1	1.6
<i>Hipposideros maggietaaylorae</i>	2	1.9–4.9	3.3	0	0	2	2.7
<i>Hipposideros obscurus</i>	4	1.1–2.9	1.8	1	0	3	0.7
<i>Hipposideros papua</i>	1	1.5–2.1	1.8	0	0	1	0.6
<i>Hipposideros pygmaeus</i>	4	1.0–3.3	2.0	4	0	0	1.5
<i>Hipposideros ruber</i>	4	0.9–2.1	1.4	2	0	2	0.6
<i>Hipposideros sabanus</i>	1	0.5–3.0	1.8	1	0	0	2.5
cyclops group							
<i>Hipposideros cyclops</i>	3	3.2–5.7	4.8	2	0	1	0.9
<i>Hipposideros muscinus</i>	1	3.5	3.3	0	1	0	—
<i>Hipposideros semoni</i>	1	2.6	2.6	0	1	0	—
diadema group							
<i>Hipposideros commersoni</i>	7	2.5–5.9	4.2	1	4	2	0.3
<i>Hipposideros diadema</i>	9	3.0–8.0	4.9	2	3	4	1.2
pratti group							
<i>Hipposideros pratti</i>	3	1.5–6.6	4.1	1	2	0	1.1
speoris group							
<i>Hipposideros larvatus</i>	5	1.6–7.4	3.4	0	1	4	2.8
<i>Hipposideros speoris</i>	1	0.7–2.4	1.6	1	0	0	1.7

^a The classification presented here is that of Koopman (in press).

parous females the nipples are more heavily pigmented, appearing in varying shades of brown. In all species the oldest females with the largest nipples also have the darkest nipples, which may be almost black in some individuals.

One of the most striking features of pubic nipples in hipposiderines is the discrepancy in size between right and left nipples in the majority of parous females. 61% of the parous hipposiderines examined in this study exhibit asymmetrical development of the pubic nipples, compared with only 3% of the rhinolophines (fig. 6; tables 4, 6). Neither side of the body appears favored when the entire sample of hipposiderines is considered (fig. 6). Interestingly, the proclivity toward asymmetrical development of the pubic nipples is a feature that may be limited to *Coelops*, *Aselliscus*, and *Hipposideros* within Hipposiderinae. None of the parous individuals of *Cloeotis*, *Rhinonycteris*, *Triaenops*, and *Asellia* that I examined have asymmetrical pubic nipples, although the sample sizes for these taxa are admittedly quite small.

Underlying causes of this marked pattern of nipple asymmetry are unclear. Assuming that pubic nipples increase in size principally as a result of use (a hypothesis that remains to be tested), it seems most likely that asymmetry in pubic nipples is produced by preferential use of one nipple by nursing young. Why this occurs widely in hipposiderines but not in rhinolophines or other bats is unclear. Fecundity is apparently similar in rhinolophines and hipposiderines, with a single young produced once a year (Brosset, 1962b, 1963; Tuttle and Stevenson, 1982). Patterns of survivorship may play a role in producing patterns of nipple asymmetry since a larger proportion of older bats (which presumably have had more offspring) have asymmetrical nip-

ples than younger individuals. Differences in nipple function might also be important if pubic nipples in some species regularly produce milk (enticing the offspring to use both nipples) while others do not, or if right and left nipples produce different amounts of milk. Another important factor may be the female preference—mother bats may encourage their offspring to adopt a particular posture (and use a specific pubic nipple) during roosting and/or flight. Female great apes (including humans) exhibit a strong preference for holding their infants on a particular side of the body, most often the left (Rheingold and Keene, 1965; Manning and Chamberlain, 1990). While bats do not show this left-side bias (fig. 6), strong individual preference for carrying offspring on a particular side of the body may account for the asymmetry observed in pubic nipples. More detailed studies of pubic nipple function and patterns of maternal care will be necessary before the underlying causes of nipple asymmetry can be adequately addressed.

All male hipposiderines examined in the current study exhibited well-developed pubic nipples with the exception of a few individuals of *Asellia tridens* and *Aselliscus stoliczkanus* that lacked any evidence of pubic nipples (table 5). Unlike rhinolophines, hipposiderine males typically have relatively large, ridgelike or flaplike pubic nipples that always project from the body wall. These are lightly pigmented and equivalent in size and shape to those of nulliparous females. As in nulliparous females, pubic nipples in hipposiderine males show the same level of development as the thoracic nipples.

VESPERTILIONIDAE

This cosmopolitan family comprises over 300 species referred to 5 subfamilies (Koop-

←

^b N is the number of individuals measured (the number of nipples = 2N). See Appendix for a list of the specimens measured.

^c Nipple length was measured from the ventral body wall to the tip of the nipple; measurements are given in millimeters and were recorded to 0.1 mm.

^d L refers to the left pubic nipple and R refers to the right pubic nipple of a single individual. "L > R" indicates the number of individuals in which the left nipple is longer than the right; "L = R" indicates the number of individuals in which the nipples are subequal; and "L < R" indicates cases in which the right nipple is longer than the left. Mean difference in length between the right and left nipples was calculated for N parous individuals.

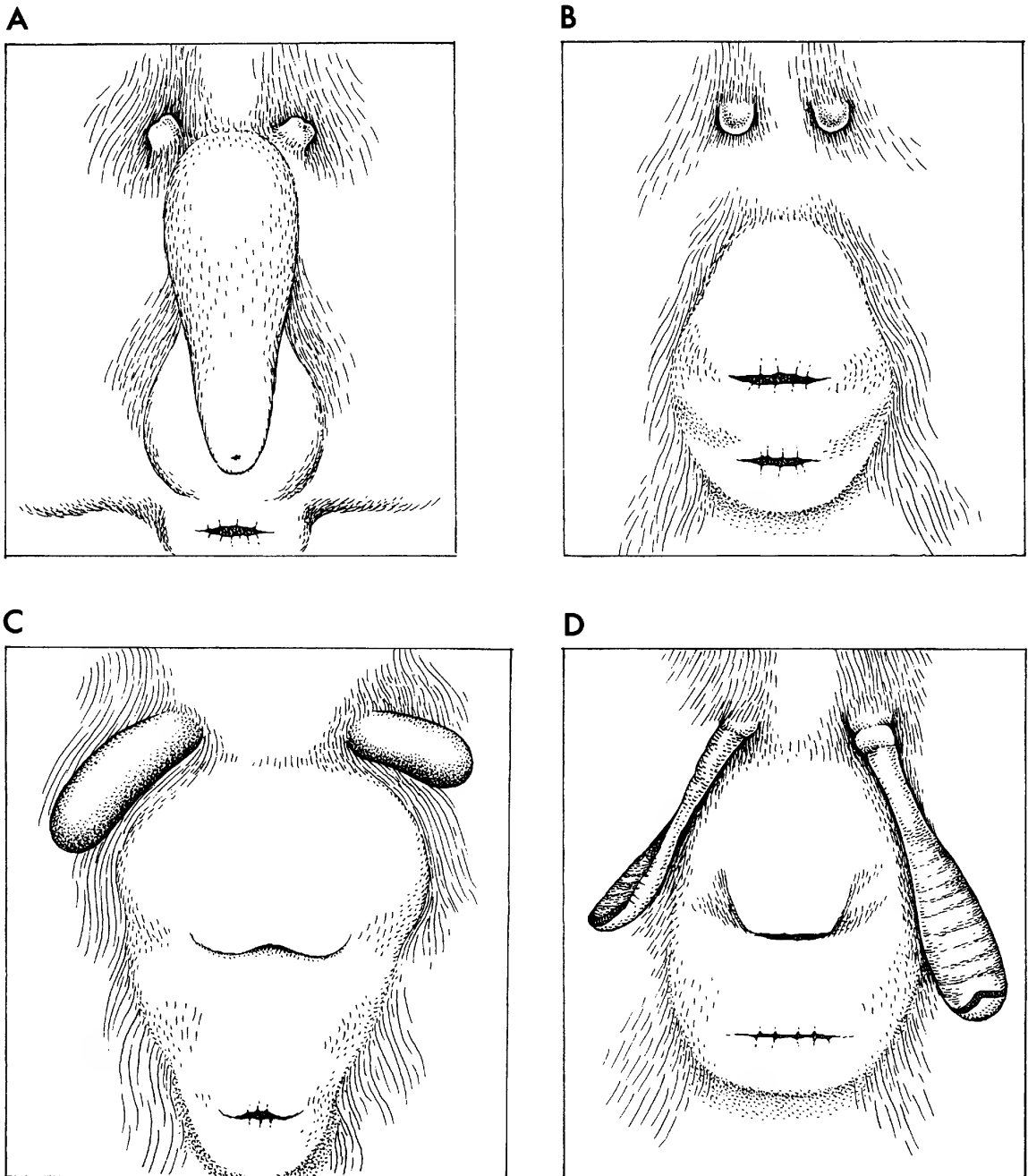


Fig. 4. Pubic nipples in *Hipposideros diadema*. A. Adult male (AMNH 196646). The flaplike pubic nipples in this individual are folded anteriorly, thus exposing the posterior surfaces of the nipples. B. Nulliparous female (AMNH 234150). The nipples in this individual are folded posteriorly to expose the anterior surfaces of the nipples. Note the similarity in size and shape between the pubic nipples of nulliparous female (B) and male (A) individuals. C. Parous female (AMNH 234152). Although not visible in this illustration, microscopic examination reveals presence of perforations in the tips of both nipples. Note that slight asymmetry in nipple length is apparent in this individual. D. Old parous female (AMNH 202247). The right nipple of the bat has been slightly twisted to expose the anterior surface of the nipple; the left nipple is positioned to show the posterior surface. A keratinous sheath can be seen on the tips of both nipples. Note that nipple asymmetry is much more pronounced in this individual than in the younger parous female shown in C.

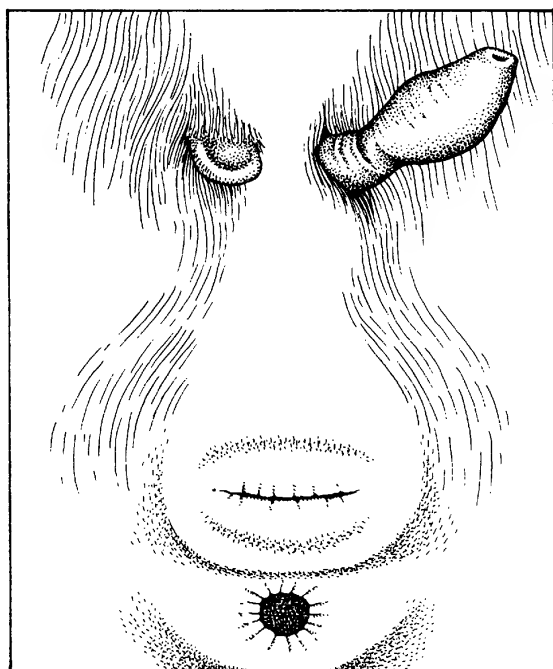


Fig. 5. Pubic nipples of parous female *Aselliscus stoliczkanus* (FMNH 38990). This is one of the most pronounced cases of pubic nipple asymmetry found among the hipposiderines examined in this study.

man, 1993). Among vespertilionids, only “Nyctophilinae” has been reported to have pubic nipples (Ryberg, 1947). This taxon, which contained 10 extant species referred to 4 genera (e.g., Hill and Smith, 1984), is no longer recognized because it appears to be polyphyletic; members of this subfamily are now referred to Vespertilioninae (Koopman, 1993, personal commun.).

Ryberg (1947) was initially responsible for the report of pubic nipples in “nyctophilines,” an observation cited subsequently by Quay (1970), Hill (1974), and Racey (1988). Unfortunately, Ryberg (1947) did not specify the source of his data, and no other published accounts have documented the occurrence of pubic nipples in “nyctophilines.” My examination of 68 female “nyctophilines” representing 8 species failed to reveal pubic nipples in even a single individual (see Appendix). Similarly, representatives of other vespertilionid subfamilies were also found to lack pubic nipples. As in the case of Nycteridae, it now seems likely that Ryberg (1947) was mistaken; there is no reason to believe

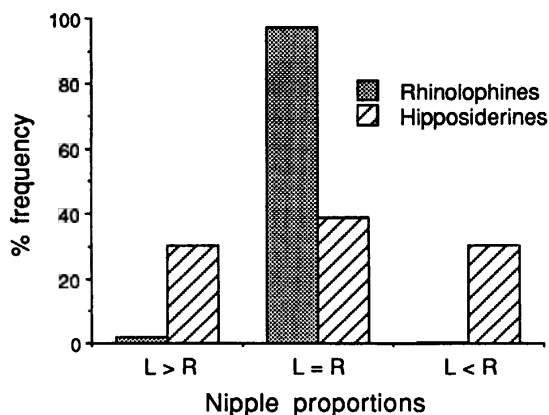


Fig. 6. Frequency of asymmetry in pubic nipple development in parous female Rhinolophinae and Hipposiderinae. Data from 182 parous female rhinolophines (table 4) and 118 hipposiderines (table 6) are included in this graph. L > R refers to individuals in which the left nipple is longer than the right; L = R indicates that the nipples are subequal; and L < R indicates cases in which the right nipple is longer than the left.

that pubic nipples occur in “nyctophilines” or any other vespertilionids.

PHYLLOSTOMIDAE

This diverse neotropical family includes approximately 50 genera and 140 species (Koopman, 1993). As mentioned previously, Ryberg (1947) suggested that pubic nipples might occur among phyllostomid bats. Although this suggestion has been cited by subsequent authors (e.g., Quay, 1970; Hill, 1974; Racey, 1988), pubic nipples have yet to be documented within Phyllostomidae despite numerous systematic and ecological studies of various species. My examination of 130 females representing 26 genera in 8 subfamilies (see Appendix) failed to reveal pubic nipples in a single individual. It seems unlikely that pubic nipples occur among phyllostomid bats, given the evidence currently available.

OTHER BAT FAMILIES

Pubic nipples have never been reported among the remaining families of bats (Pteropodidae, Noctilionidae, Mormoopidae, Natalidae, Furipteridae, Thyropteridae, Myzopodidae, Mystacinidae, and Molossidae).

Although only a few representatives of each family were included in the current study (see Appendix), my examination of parous females confirmed the uniform absence of pubic nipples in all of the families listed above.

FUNCTION OF PUBIC NIPPLES IN BATS

The most obvious function for nipples of any kind is to transfer milk from a lactating mother to her offspring. Pubic nipples in bats, however, are widely regarded to function solely as a device for attaching the young to the mother: e.g., pubic nipples "... do not secrete milk, but serve as a holdfast for the young bat while the mother is in flight" (Hill and Smith, 1984: 31). This "holdfast" hypothesis is an oversimplification; while support of the young during flight is clearly one function, nutritive and other functions may be relevant in some or all taxa.

It is very difficult to assess the lacteal function of pubic nipples using only museum specimens. Preservation in formalin and alcohol variably shrinks soft tissues, and abdominal incisions made for the purposes of preservation frequently intersect the pubic nipples. If gross morphology is used to assess possible lacteal function of pubic nipples (as in this study), lactating females must be examined in order to confirm presence/absence of a duct system and lacteal tissue. Unfortunately, well-preserved lactating females are relatively rare in museum collections. Histological studies of pubic nipples and associated structures would be of great value, but such work has not yet been done. Given these limitations, only a few inferences concerning function can be drawn from the current study.

As described above, pubic nipples contain duct systems and appear to communicate with a small amount of lacteal tissue in many species of bats (e.g., *Rhinopoma microphyllum*; *Rhinolophus cornutus*; *Hipposideros diadema*). All clearly lactating rhinopomatids, rhinolophines, and hipposiderines examined in this study showed some evidence of lacteal function in the pubic nipples. The only taxonomic groups in which pubic nipples do not appear to function in lactation are Craseonycteridae and Megadermatidae, although more work on both taxa will be necessary to

verify this hypothesis. In those forms where pubic nipples provide no (or insufficient) milk, young bats attached to a pubic nipple must return to the thoracic nipples to nurse. Brosset (1963) observed alternating use of thoracic and pubic nipples in *Megaderma spasma*, *Hipposideros speoris*, *Rhinolophus rouxi*, and *R. luctus*, and Vaughan and Vaughan (1987) reported this behavior in *Lavia frons*. However, it should be noted that infants might alternate between sets of nipples even if both sets can provide milk. The observation that young bats switch nipples does not necessarily indicate that pubic nipples do not function in lactation.

Several authors have reported that offspring born to mothers with pubic nipples remain attached to the thoracic nipples for the first few weeks after birth. Gaur and Shahrokh (1989) reported that infant *Rhinopoma microphyllum* remain on the mother's breast suckling milk from the thoracic nipples for the first 2–3 weeks of life. Similarly, the pubic nipples of *Hipposideros ater* apparently are not used until the young are big enough to crawl around on the mother (Strahan, 1983). Because young bats appear to nurse exclusively from the thoracic nipples in the first few weeks of life, and only later switch to the pubic nipples, Gaur and Shahrokh (1989) suggested that the mammary glands of these regions may start functioning at different times. Again, comprehensive field and/or laboratory studies will be necessary to test this hypothesis.

Other substances besides milk may be secreted by the pubic nipples. Kolenati (1857) apparently succeeded in squeezing lymph from the pubic nipples of *Rhinolophus blasii* and concluded that pubic nipples normally secrete lymph. He subsequently suggested that lymph represents a less concentrated food source than milk, equivalent in some ways to colostrum. This view was countered by Jäckel (1860), who pointed out that lymph can be obtained from almost any piece of skin under sufficient pressure. Jäckel (1860) surmised that the function of pubic nipples was to provide the young with a holdfast other than the thoracic nipples so as to prevent the mother from being sucked dry by her offspring. Yet another possible function of pubic nipples involves production of odors. Tem-

minck (1841) reported emission of an evil-smelling substance from the pubic nipples of an unidentified rhinolophid. Because scent glands are important in most bats, odor production might prove to be an important function of the pubic nipples in some taxa (Ryberg, 1947).

Unfortunately, all of the above conjectures are supported by insufficient data. We do not yet know if the lacteal tissue associated with some pubic nipples produces measurable quantities of milk, and we do not know if other substances are regularly secreted by the pubic nipples. Detailed field and laboratory studies—including histological and biochemical analyses—will be required to resolve these issues.

There is little doubt that an important function of pubic nipples is to provide a hold-fast for nursing young. Infant bats are equipped with sharp, recurved deciduous teeth unlike the milk dentition of other mammals (Leche, 1875; Matthews, 1950; Friant, 1951; Simmons, in prep.). Immediately after birth, young bats firmly grasp one of their mother's nipples and they can be dislodged only with considerable difficulty (Racey, 1988; personal obs.). When frightened, young bats attached in such a fashion may cause the mother some discomfort, possibly because the teeth actually puncture the mother's skin. Cooperation of the offspring appears to be necessary to disengage the nipple under these circumstances (personal obs.).

Young bats of all taxa apparently adopt a similar posture when using a pubic nipple: the head of the offspring is directed in the opposite direction from that of the mother (fig. 7; Ryberg, 1947; Brosset, 1962d, 1963; Strahan, 1983; Vaughan and Vaughan, 1987; Gaur and Shahrokh, 1989; Duangkhae, 1990). The nipple is grasped in the mouth of the young bat, which additionally clings to the mother either by grasping her fur with its feet or by wrapping its hind legs around her neck (fig. 7). Offspring clinging by wrapping their legs around the neck of the mother has been reported in several taxa including *Rhinopoma microphyllum* (fig. 7; Gaur and Shahrokh, 1989), *Craseonycteris thonglongyai* (Duangkhae, 1990), and *Lavia frons* (Vaughan and Vaughan, 1987). Strahan (1983) reported that young *Rhinolophus megaphyllus* instead

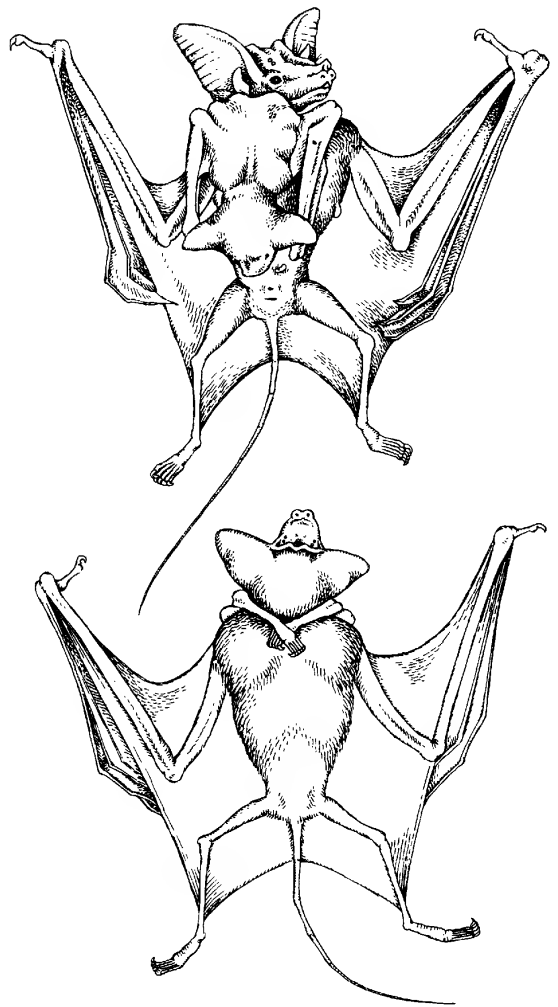


Fig. 7. Two views of a lactating *Rhinopoma microphyllum* with her offspring attached to a pubic nipple (drawn from a photograph in Gaur and Shahrokh [1989] using AMNH 212070 as a reference for anatomical details). Note that the hind legs of the young bat are locked around the neck of the mother. This behavior has also been reported in *Craseonycteris thonglongyai* (Duangkhae, 1990) and *Lavia frons* (Vaughan and Vaughan, 1987).

cling by using their feet to grasp the mother's fur, but it is possible that he observed infants too small to effectively reach around the neck of the mother. With her young attached to a pubic nipple a mother bat can fly carrying an offspring that is almost as large as she is (Brosset, 1962b, 1963).

It has been suggested that pubic nipples may provide a kind of substitute for the pro-

tective support provided the offspring by the uropatagium in other bats (Ryberg, 1947). Some bats with a large uropatagium and a long tail (e.g., vespertilionids, thyropterids) can cup the uropatagium ventrally to partially shield the offspring. This is not possible for rhinopomatids, which have a long tail but a narrow uropatagium. Craseonycterids and megadermatids have a large uropatagium, but the tail is either short or absent. Rhinolophids have short tails and can cup the uropatagium dorsally, but they cannot cup it ventrally (Ryberg, 1947). All of the bats that have pubic nipples lack the ability to cup the uropatagium ventrally to help support their offspring. However, pubic nipples are absent in other bats that lack this "cupping" ability (e.g., many phyllostomids), so no clear correlation exists among these features. It seems more likely that carrying young attached to the pubic nipples affects the equilibrium of the mother, perhaps making it easier for her to carry her offspring while in flight (Brosset, 1962b). Brosset (1962b) noted that the young are virtually always carried attached to the pubic nipples when these nipples are present.

It also seems clear from field observations that the preferred roosting position for young bats is the "head-up" posture afforded by attachment to a pubic nipple. Because adult bats roost in a "head-down" position, attachment to a thoracic nipple results in the head of the infant being directed either down or laterally, while use of a pubic nipple directs the infant's head upward (Brosset, 1962d, 1963). The body and wings of a young bat roosting in the "head-up" position rest against the chest of the mother (fig. 7). This roosting posture has been noted in young *Rhinopoma* (Gaur and Shahrokh, 1989), *Craseonycteris* (Duangkhae, 1990), *Megaderma* (Brosset, 1962d, 1963), *Lavia* (Vaughan and Vaughan, 1987), *Rhinolophus* (Brosset, 1962b, d, 1963; Strahan, 1983), and *Hipposideros* (Brosset, 1962b, d, 1963; Strahan, 1983). It is not clear if this behavior principally affords advantages to the offspring (in terms of thermoregulation, for example) or if it simply facilitates a quick getaway if the mother and offspring are threatened.

There is no evidence that the pubic nipples of male bats function in lactation or as hold-fasts for the young. In over 10 years of field-

work on Indian megadermatids, rhinolophines, and hipposiderines, Brosset (1962a, b, c, d, 1963) never witnessed male bats associating with or carrying young. Most workers agree that care of the young is provided exclusively by the female in all bat species (Hill and Smith, 1984). It is possible, however, that the pubic nipples secrete something (perhaps odiferous fluids) in some males. This seems most likely in hipposiderines, which typically exhibit the greatest development of male pubic nipples. Obviously, more laboratory and fieldwork is necessary to evaluate this conjecture.

PHYLOGENETIC INTERPRETATION

WHAT IS THE PRIMITIVE PATTERN FOR BATS?

As mentioned previously, the majority of bats exhibit only a single pair of nipples that are located on the thorax. An additional pair of thoracic nipples are known to occur only in two closely related genera of vespertilionid bats: *Lasiurus* (including *Dasypterus*) and *Otonycteris* (Allen, 1880; Lyon, 1903; Ward, 1905; Ryberg, 1947; Goodwin and Greenhall, 1961; Quay, 1970; Racey, 1988). A third pair of nipples may also occasionally develop in these taxa (Racey, 1988). None of these nipples occur in the abdominal region, and there is no reason to believe that they are homologous with the pubic nipples. The increase in number of thoracic nipples is associated with increased litter size. Lasiurine bats commonly have three or four offspring per reproductive cycle, as opposed to one or sometimes two offspring in megachiropterans and other microchiropteran bats (Carter, 1970; Quay, 1970; Tuttle and Stevenson, 1982). These patterns (i.e., two or three pairs of thoracic nipples, three or four offspring per cycle) appear to be derived *within* vespertilionids, well within the microchiropteran clade. In the thoracic region, a single pair of nipples appears to represent the primitive condition for Chiroptera. This also seems to be true of the potential sister taxa of Chiroptera (see discussion below).

Abdominal nipples are somewhat more difficult to interpret. As described above, pubic nipples appear ubiquitous in females of four families of bats (Rhinopomatidae, Craseo-

nycteridae, Megadermatidae, and Rhinolophidae [including Hipposiderinae]), but are absent in Megachiroptera and the remaining microchiropteran families. When present, pubic nipples always occur as a single pair (the only exception being one female *Macroderma gigas* with a single supernumerary nipple), and they are located in a similar position near the pubes in all taxa. Similarity of these structures across diverse taxa suggests that they are homologous. Assuming that Microchiroptera, Megachiroptera, and Chiroptera are each monophyletic (sensu Wible and Novacek, 1988; Novacek, 1990; Adkins and Honeycutt, 1991, 1993; Mindell et al., 1991; Thewissen and Babcock, 1991, 1993; Ammerman and Hillis, 1992; Bailey et al., 1992; Kay et al., 1992; Stanhope et al., 1992, 1993; Beard, 1993; Johnson and Kirsch, 1993; Lockett, 1993; Simmons, 1993; Szalay and Lucas, 1993; Wible and Martin, 1993), two principal hypotheses must be considered with regard to the evolution of pubic nipples in bats. Either (1) presence of pubic nipples is primitive for Chiroptera, and these structures were lost in Megachiroptera and within Microchiroptera, or (2) absence of pubic nipples is primitive, and they evolved within the microchiropteran lineage. If pubic nipples evolved within Microchiroptera, the possibility that they evolved more than once must also be considered. To evaluate various alternative hypotheses, it is necessary to consider outgroups, a difficult proposition considering the diversity of opinions concerning bat relationships.

Dermoptera (gliding lemurs), Primates, and Scandentia (tree shrews) are the groups most often mentioned as possible sister taxa of Chiroptera (e.g., Wible and Novacek, 1988; Novacek, 1990; Mindell et al., 1991; Kay et al., 1992; Beard, 1993; Johnson and Kirsch, 1993; Simmons, 1993; Szalay and Lucas, 1993). Dermopterans lack abdominal nipples and have only a single pair of thoracic nipples located in the axillary region (Nowak, 1991). Among primates, only a few strepsirrhines have more than one pair of nipples. Cheirogaleids have three pairs (one thoracic and two abdominal), as do members of the lemurid genus *Varecia* (Nowak, 1991). Anthropoids, tarsiers, most lemurids, all lorises, megaladapids, indriids, and dauben-

toniids lack abdominal nipples and have a single pair of thoracic nipples (Nowak, 1991). Among lemuriform primates, cheirogaleids and *Varecia* are not believed to be particularly closely related, and neither appears at the base of the lemuriform clade (Schwartz, 1992; Tattersall and Schwartz, 1992). Regardless of the perceived affinities of tarsiers, the taxonomic distribution of nipple patterns suggests that presence of a single pair of thoracic nipples—and absence of abdominal nipples—is primitive for Primates (= Euprimates in the context of the current study). It is more parsimonious to hypothesize a convergent increase in nipple number in two groups (*Varecia* and cheirogaleids) than a loss of nipples in numerous lineages.

Tree shrews (order Scandentia) vary considerably in number and position of nipples. *Ptilocercus*, the sole member of the subfamily Ptilocercinae, has two pairs of thoracic nipples (Lyon, 1913). Among tupaiines, *Lyonogale* and *Urogale* also have two pairs of nipples in the same locations (Lyon, 1913). *Dendrogale* has only one pair of nipples, which are abdominal, but *Anthana* has three pairs, one thoracic and two abdominal (Lyon, 1913). Species of *Tupaia* generally have two pairs of thoracic nipples (e.g., *T. javanica*, *T. minor*, *T. palawanensis*, *T. splendidula*, *T. montana*, and *T. picta*) but there are some exceptions (Lyon, 1913). *T. nicobarica* has only one pair of thoracic nipples, while *T. belangeri* and *T. longipes* have two thoracic plus one abdominal pair (Lyon, 1913). Various taxa currently recognized as synonyms or subspecies of *Tupaia glis* (Wilson, 1993) also exhibit different nipple patterns. Members of Lyon's "*ferruginea* or *glis*" and "*splendidula*" species groups² have two pairs of thoracic

² Lyon (1913) recognized 48 named forms of *Tupaia* that he arranged into a hierarchical series of sections, groups, and subgroups. All 14 members of Lyon's "*ferruginea* or *glis*" species group are now placed in *Tupaia glis* (Wilson, 1993). The nominal species from Lyon's "*hypochrysa*" and "*discolor*" groups are also placed in *Tupaia glis*, along with five members of the "*splendidula*" group (*T. chrysomalla*, *T. riabus*, *T. anambae*, *T. castanea*, *T. siaca*). The remaining members of these groups are now considered to represent species distinct from *glis* (e.g., *T. chyrogastrer*, *T. longipes*, and *T. splendidula*; Wilson, 1993).

TABLE 7
A Higher-Level Classification of Recent Bats
(from Koopman, 1984)

Order Chiroptera
Suborder Megachiroptera
Family Pteropodidae
Suborder Microchiroptera
Infraorder Yinochiroptera
Superfamily Emballonuroidea
Family Emballonuridae
Family Craseonycteridae
Family Rhinopomatidae
Superfamily Rhinolophoidea
Family Nycteridae
Family Megadermatidae
Family Rhinolophidae
Subfamily Rhinolophinae
Subfamily Hipposiderinae
Infraorder Yangochiroptera
Superfamily Phyllostomoidea
Family Mormoopidae
Family Noctilionidae
Family Phyllostomidae
Superfamily Vespertilionoidea
Family Thyropteridae
Family Myzopodidae
Family Furipteridae
Family Mystacinidae
Family Natalidae
Family Molossidae
Family Vespertilionidae

nipples, *T. glis hypochrysa* is characterized by one pair of thoracic nipples, and *T. glis discolor* has two thoracic plus one abdominal pair (Lyon, 1913). These apparently fixed differences in nipple number suggest that the latter taxa may represent species distinct from *glis*.

The distribution of various nipple patterns among tree shrews makes it difficult to estimate the primitive condition for Scandentia. Luckett (1980b) estimated that three pairs of nipples is primitive for tree shrews, but this hypothesis seems unlikely given the phylogenetic relationships proposed by Luckett (1980a: fig. 7): (*Ptilocercus* (*Dendrogale* (*Urogale* (*Anathana* (*Lyonogale*, *Tupaia*))))). Assuming monophyly of Scandentia (demonstrated by Zeller, 1986), mapping the distribution of abdominal and thoracic nipples on Luckett's (1980a) phylogenetic tree suggests that presence of two pairs of nipples (one thoracic and one abdominal) is probably the primitive condition for tree shrews.

Given the nipple patterns described above,

interpretation of polarity of transformation in pubic nipples in bats depends upon the outgroup relationships assumed. If Megachiroptera and Dermoptera are assumed to represent consecutive sister taxa of Microchiroptera (sensu Wible and Novacek, 1988; Novacek, 1990; Johnson and Kirsch, 1993; Simmons, 1993; Szalay and Lucas, 1993), absence of pubic nipples appears to be primitive for Chiroptera and for the lineage leading to Microchiroptera. This also holds if a clade containing Primates + Dermoptera is considered to represent the sister group of bats (sensu Beard, 1993). If a larger clade containing Primates + Dermoptera + Scandentia is the sister group of bats (sensu Ammerman and Hillis, 1992), or if a clade containing Primates + Scandentia is the sister group of bats (sensu Kay et al., 1992), the polarity of transformation in pubic nipples is ambiguous. No arrangement of outgroups unambiguously supports the hypothesis that *presence* of pubic nipples is primitive for bats. In part because pubic nipples do not occur in Megachiroptera, the best working hypothesis seems to be that *absence* of pubic nipples is primitive for Chiroptera; this assumption will be accepted for the remainder of this discussion.

PUBIC NIPPLES AND PHYLOGENY OF MICROCHIROPTERA

Phylogenetic relationships among families of microchiropteran bats have been debated extensively in recent literature, but no consensus has yet emerged (Smith, 1976; Van Valen, 1979; Novacek, 1980; Pierson, 1986; Griffiths and Smith, 1991; Griffiths et al., 1992). In this context, the taxonomic distribution of pubic nipples may contribute to our understanding of higher-level relationships of microchiropteran bats. The classification of Koopman (1984) will be accepted for the purposes of providing superfamilial group names for the following discussion (table 7).

The only previous attempt to interpret pubic nipples in a phylogenetic framework was that of Van Valen (1979), who included pubic nipples as a character in his analysis of higher-level bat relationships. The sources of Van Valen's data appear to have been Quay (1970) and Hill (1974), who incorrectly stated that pubic nipples were present in nycterids. Based

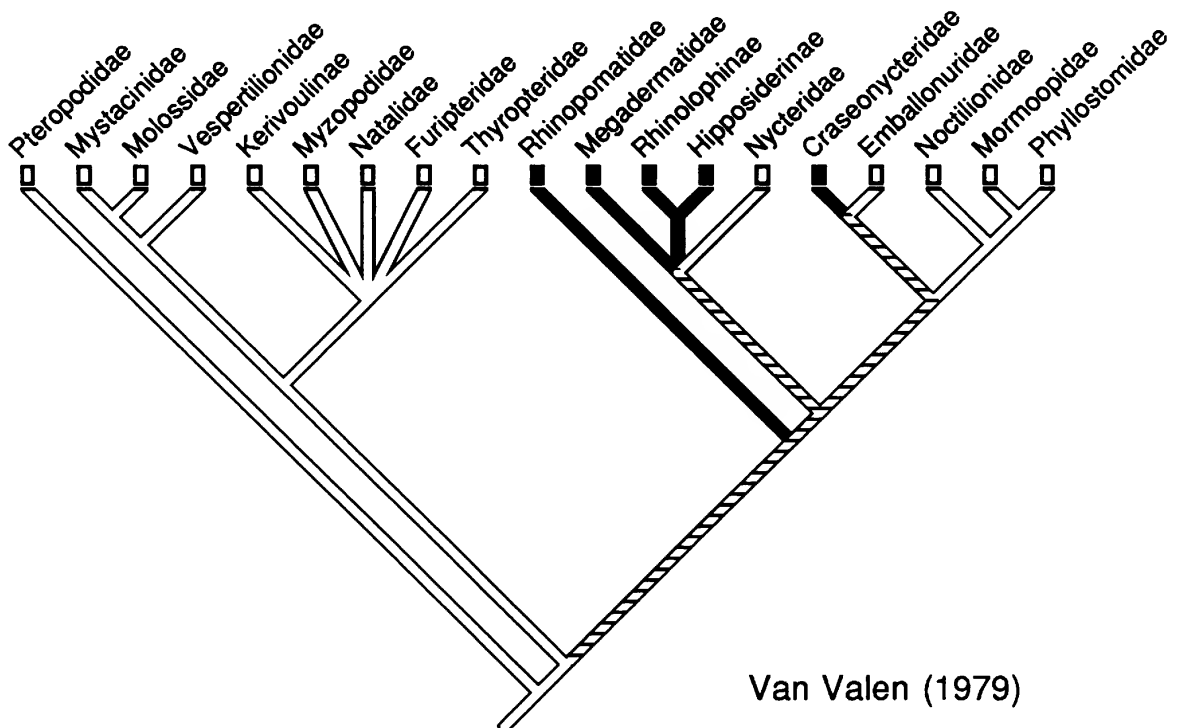


Fig. 8. Distribution of pubic nipples mapped on the phylogeny of Chiroptera proposed by Van Valen (1979). The data shown have been corrected based on the results of the current study; see text for a discussion of the evolutionary transformations implied by this phylogeny. In this tree and those in the following figures, presence of pubic nipples is indicated by black boxes, and lineages presumed to have pubic nipples are indicated by black shading on the branches. Absence of pubic nipples is indicated by white boxes and white shading. Crosshatching indicates parts of the tree where presence or absence of pubic nipples could not be reconstructed unambiguously. The rank endings of various taxonomic names (e.g., Hipposiderinae versus Hipposideridae) have been portrayed as originally presented by each author.

on a preferred phylogeny of bats that he developed using unspecified cladistic methods, Van Valen (1979) indicated that pubic nipples evolved in the common ancestor of rhinolophoid + emballonuroid + phyllostomoid bats, only to be lost independently in emballonurids and phyllostomoids. Absence of pubic nipples in the common ancestor of all bats—and in the most recent common ancestor of Microchiroptera—was implied by this hypothesis.

Van Valen's (1979) original interpretation required three evolutionary "steps" to explain the distribution of pubic nipples in bats—one origination event (appearance of pubic nipples early in microchiropteran evolution) and two reversals (loss of pubic nipples, once in emballonurids and once in phyllostomoids). If the data are adjusted to take into account the absence of pubic nipples in

Nycteridae (fig. 8), interpretation of transformations in pubic nipples becomes more ambiguous because several equally parsimonious hypotheses must be considered. For example, a single origination event followed by separate reversals in Nycteridae, Emballonuridae, and Phyllostomoidea requires four evolutionary steps, as does independent evolution of pubic nipples in each of the four families known to have pubic nipples.

In recent years a number of hypotheses of interfamilial relationships of bats have been presented based on data ranging from skull morphology to immunological distances. Assuming that absence of pubic nipples is primitive for bats, mapping the distribution of pubic nipples on different phylogenies results in very different interpretations of this character.

Smith (1976: 56) presented a cladogram of

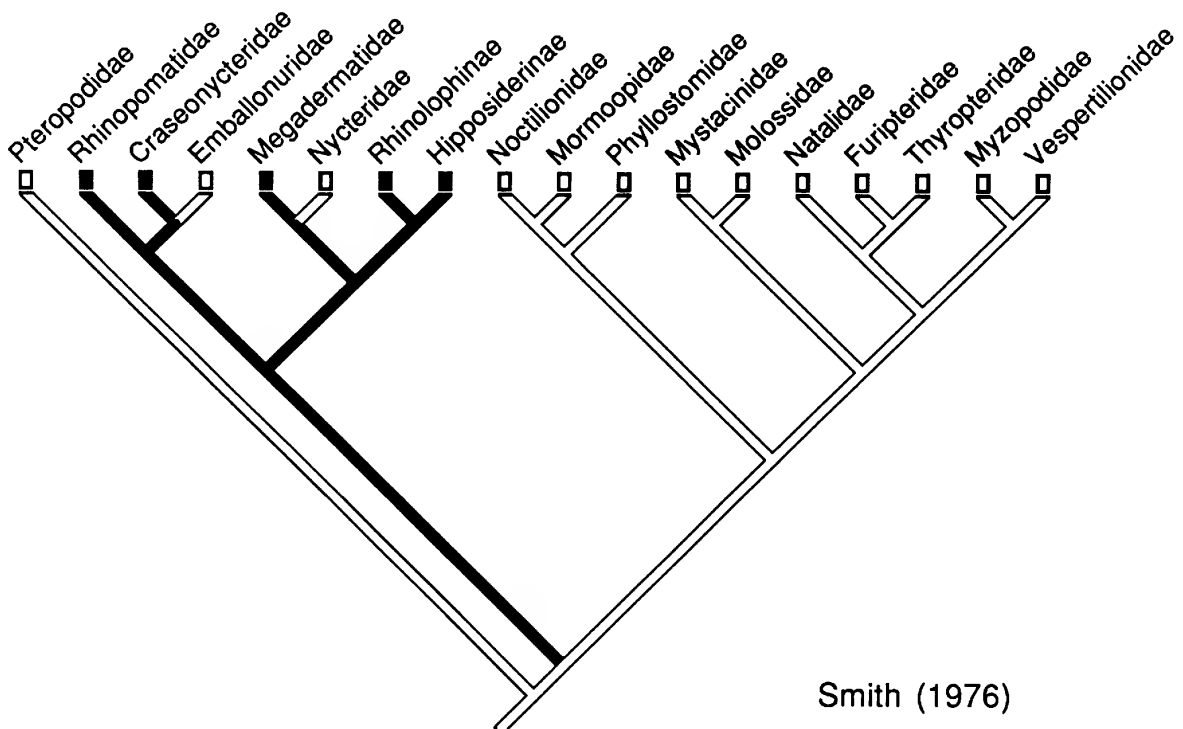


Fig. 9. Distribution of pubic nipples mapped on the phylogeny presented by Smith (1976). Three evolutionary events are necessary to explain the pattern of pubic nipple distribution given this phylogeny. Pubic nipples appear to have evolved only once (in the lineage leading to Emballonuroidea + Rhinolophoidea), but two reversals are indicated (one in Emballonuridae and one in Nycteridae).

bat families that was intended to represent the "generally accepted view" of bat phylogeny. This phylogeny was presumably based principally on consideration of features of skin and skull morphology. In the context of Smith's phylogeny (fig. 9), the most parsimonious interpretation of pubic nipples is that they evolved only once, in the common ancestor of Yinochiroptera. Reversals must be postulated to have occurred twice, once in Emballonuridae and once in Nycteridae.

Novacek (1980) analyzed chiropteran relationships using characters of the auditory region. The cladogram produced in his study departed significantly from previous hypotheses of interfamilial relationships, and Novacek (1980) warned against using this cladogram as a basis for a new phylogenetic reconstruction or classification. Nevertheless, Novacek's (1980) cladogram offers an opportunity to investigate congruence between pubic nipples and another character system, i.e., auditory features. Mapping the

distribution of pubic nipples on this tree (fig. 10) indicates that there is no congruence; even though Craseonycteridae was not included in Novacek's tree, the most parsimonious arrangement involves at least four steps (e.g., independent evolution of pubic nipples in Rhinopomatidae, Megadermatidae, Rhinolophidae, and Hipposideridae). Examination of the distribution of the auditory characters described by Novacek (1980) reveals that none are fully congruent with the distribution of pubic nipples.

A very different phylogeny of bats was proposed by Pierson (1986) on the basis of immunological distance data. Unfortunately, Pierson's (1986) study did not include representatives of Nycteridae or Craseonycteridae. Nevertheless, this phylogeny is intriguing from the perspective of pubic nipples. If Pierson's (1986) phylogeny is accepted, only one evolutionary step is required to explain the distribution of pubic nipples (fig. 11); presence of pubic nipples is interpreted as a

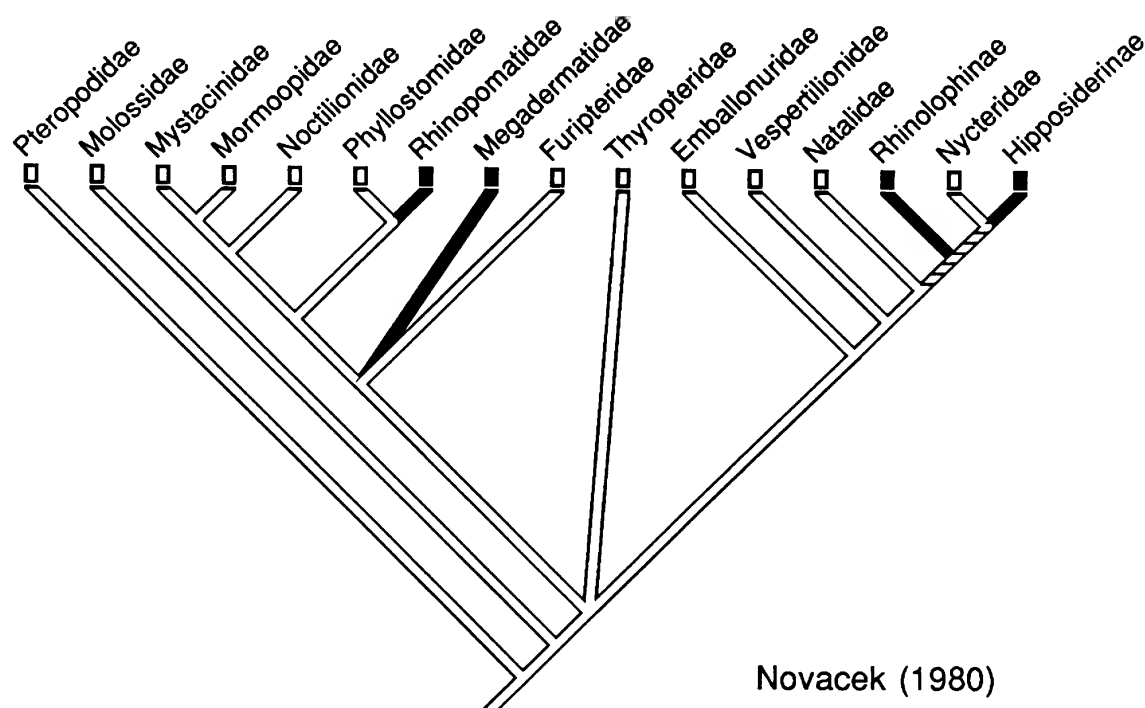


Fig. 10. Distribution of pubic nipples mapped on a phylogenetic tree derived from auditory characters (Novacek, 1980). Even in the absence of Craseonycteridae (which was not included in Novacek's study) at least four evolutionary events are required to explain the distribution of pubic nipples given this tree topology.

synapomorphy unequivocally diagnosing a clade containing Rhinopomatidae + Megadermatidae + Hipposideridae + Rhinolophidae. This conclusion is significant because it implies that Emballonuroidea is paraphyletic.

Griffiths and his colleagues have used musculoskeletal morphology of the hyoid region to develop hypotheses of relationships among and within various bat families. Two phylogenies relevant to interpretation of pubic nipples have been presented, one (fig. 12A) favored by Griffiths and Smith (1991) and Griffiths et al. (1992), and an alternative (fig. 12B) additionally presented by Griffiths et al. (1992). These two phylogenies are equally parsimonious with respect to the hyoid data. However, consideration of pubic nipples lends some support to the latter hypothesis over the former. If the distribution of pubic nipples is mapped on the first tree (fig. 12A), three evolutionary steps are required to explain the pubic nipple data (this can be re-

duced to two steps—an origination event and a reversal—if the cladogram is resolved to better fit the combined hyoid and pubic nipple data). In comparison, the pubic nipple data is entirely congruent with the phylogeny shown in figure 12B; only one evolutionary step (an origination event) is required. In this case pubic nipples would be interpreted as a synapomorphy diagnosing a clade containing Hipposiderinae + Rhinolophinae + Megadermatidae + Rhinopomatidae. Presence of pubic nipples in Craseonycteridae (a taxon not included in the hyoid studies) suggests that it also belongs to this clade. Again, these results suggest that Emballonuroidea is paraphyletic.

Morphological data from a variety of sources (e.g., Hill, 1974; Novacek, 1980; Griffiths et al., 1992; personal obs.) support monophyly of a clade containing Rhinopomatidae + Craseonycteridae + Megadermatidae + Rhinolophinae + Hipposiderinae. Derived character states supporting this

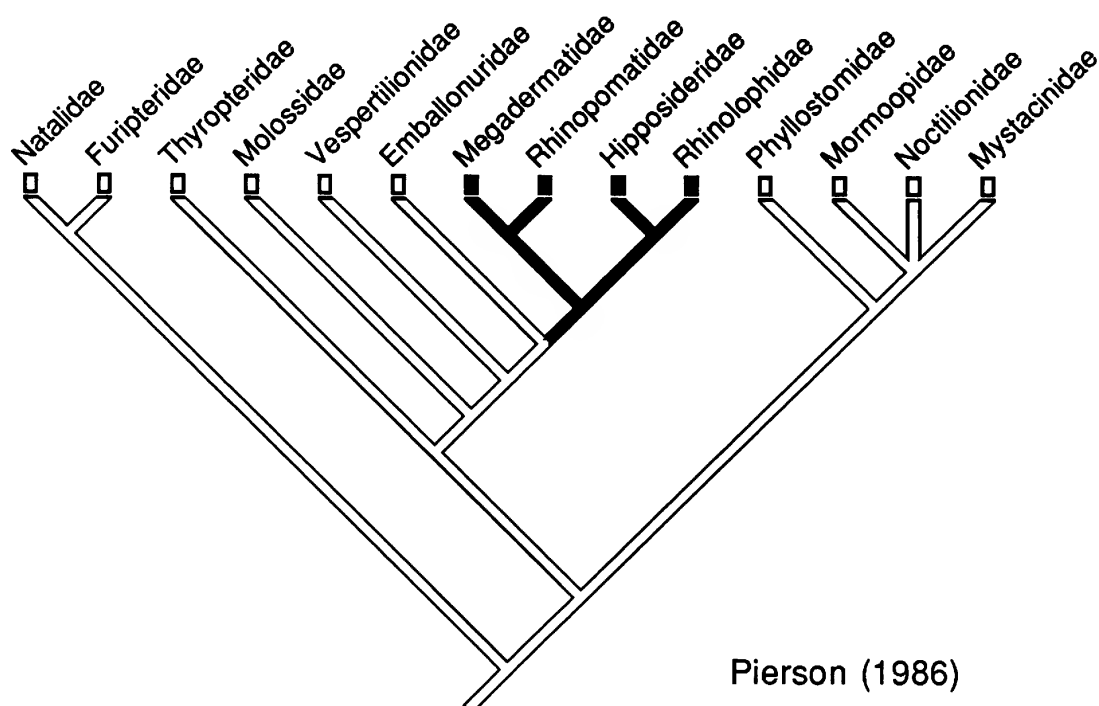


Fig. 11. Distribution of pubic nipples mapped on a phylogeny of Chiroptera proposed by Pierson (1986) on the basis of transferrin immunological distances. Note that this phylogeny unambiguously implies a single origin for pubic nipples in the lineage leading to the clade containing Rhinopomatidae + Megadermatidae + Hipposideridae + Rhinolophidae. The absence of pubic nipples in Nycteridae (not included in Pierson's study) suggests that this family would fall outside of this clade. Similarly, presence of pubic nipples in Craseonycteridae (also not included in Pierson's study) suggests that this family would fall *within* the above clade.

grouping include (1) presence of pubic nipples, (2) presence of dermal outgrowths (ridges or noseleaf) on the narial pads, (3) absence of the lower first incisor, (4) absence of the upper first incisor, and (5) presence of mandibulo-hyoideus muscle (although this character has not yet been studied in *Craseonycteris*). Pierson's (1986) immunological results are also entirely consistent with this hypothesis. However, it must be noted that other characters offer support for an alternative hypothesis, namely monophyly of a clade containing Nycteridae + Megadermatidae + Rhinolophinae + Hipposiderinae. Derived character states supporting this grouping include (1) fusion of the last cervical and first thoracic vertebrae, (2) enlargement of the first rib, and (3) semivertical orientation of the tympanic annulus. If the latter phylogenetic hypothesis is correct, pubic nipples probably evolved in the common ancestor of a clade containing Rhinopomatidae + Craseonyc-

teridae + Rhinolophoidea, and were later lost in Nycteridae, or pubic nipples evolved twice, once in a clade containing Rhinopomatidae + Craseonycteridae and again in Megadermatidae + Rhinolophidae.

The phylogenetic significance of variation in the form of pubic nipples is difficult to evaluate due to the relatively small sample sizes available for most taxa. In cases where large samples of parous females have been examined, within-species variation is often so great that most among-species differences are obscured. Polymorphism in male pubic nipples is widely distributed but does not appear to be phylogenetically significant; note the distribution of polymorphism among the various species groups of rhinolophines (table 3) and hipposiderines (table 5). Asymmetrical development of the pubic nipples is largely limited to hipposiderines (fig. 6), but small sample sizes for many taxa (particularly within Rhinonycterina) limit interpretation

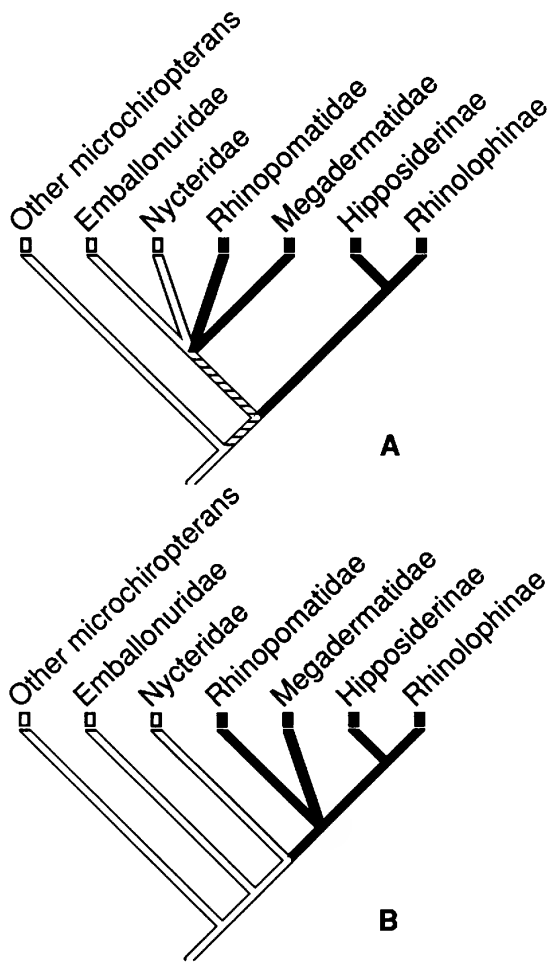


Fig. 12. Distribution of pubic nipples mapped on two phylogenies (A,B) discussed by Griffiths and Smith (1991) and Griffiths et al. (1992). Both trees are equally parsimonious in the context of the hyoid characters presented by those authors. Tree A was preferred by Griffiths and his colleagues on the basis of hypothesized patterns of transformation in two characters. Both sets of authors concluded that a reversal related to the origin of the sternohyoid (required by tree A) was more likely than a reversal related to the origin of the omohyoid (required by tree B). If the distribution of pubic nipples is taken into account, tree B is more parsimonious than tree A. At least two and perhaps three evolutionary events related to pubic nipples are required by topology of tree A; only one event is required given tree B.

of this trait. In a few cases patterns of pigmentation appear to represent autapomorphies of various species. For example, *Lavia frons* is the only megadermatid to exhibit pig-

mented nipples, and *Rhinolophus luctus* is unique in having nipples that are gray-brown with white tips. Other features of pubic nipples may prove phylogenetically informative when larger samples of parous females of closely related species are available for comparison.

CONCLUSIONS

Examination of 1722 specimens representing 206 species indicates several errors in previous descriptions of the taxonomic distribution of pubic nipples among bats. Pubic nipples appear to be present in all species belonging to the families Rhinopomatidae, Craseonycteridae, Megadermatidae, and Rhinolophidae (including Hipposiderinae). Contrary to previous reports, there is no evidence of pubic nipples in Nycteridae, Emballonuridae, Phyllostomidae, or Nyctophilinae. When present, pubic nipples are ubiquitous in females but may be absent in some males.

Studies of the gross morphology of pubic nipples suggest that they have at least some lacteal function in many bat species, but this remains to be confirmed by more detailed laboratory and field studies. We do not yet know what (if any) substances secreted by pubic nipples are actually available to young bats. The functional significance of these organs as holdfasts (e.g., in terms of energetics of roosting and flying bats) similarly remains to be explored.

The phylogenetic interpretation of pubic nipples is somewhat hampered by uncertainty concerning the relationships of bats to other mammalian orders. Based on a variety of evidence, including the absence of pubic nipples in Megachiroptera, it currently seems most likely that absence of pubic nipples is the primitive condition for bats. Because pubic nipples are ubiquitous in some families of Microchiroptera but entirely absent in others, the pattern of distribution of pubic nipples has the potential to contribute to our understanding of interfamilial relationships. Interestingly, patterns of distribution of pubic nipples are congruent with those of some morphological characters in other anatomical systems (e.g., hyoid musculature, postcranial osteology). However, more work is

necessary before these data can be productively analyzed in a comprehensive phylogenetic analysis. Careful examination of features previously described only in general literature reviews must take high priority; as demonstrated in this study, reports of taxonomic distribution patterns contained in such

works may be unreliable. No single character (such as pubic nipples) or subset of data (such as cranial morphology) holds the key to chiropteran phylogeny; rather, the future lies in integrative studies that bring together a wide variety of data from different sources.

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APPENDIX

List of Specimens Examined

The following list summarizes the taxa and specimens examined in the current study. Parous females with pubic nipples are indicated by an asterisk; see tables 2, 4, and 6 for summaries of measurements of these specimens. The classification employed is that of Koopman (1984).

Pteropodidae: Pteropodinae: *Rousettus aegyptiacus*: AMNH 257001–275002. *Rousettus amplexicaudatus*: AMNH 232512. *Pteropus tonganus*: AMNH 79986; 79989. *Dobsonia viridis*: USNM 543778. *Harpionycteris whitheadi*: USNM 459103. *Haplonycteris fischeri*: USNM 459100. **Macroglossinae:** *Macroglossus lagochilus*: USNM 543960; 543970; 544046. *Notopteris macdonaldi*: USNM 260070; 260072; 260076.

Rhinopomatidae: *Rhinopoma hardwickei*: AMNH *208125; *208126; 217292; 217294–217297; *217298; 217299–217301; 219718–219722; 244133–244134; 244404–244405; USNM 478306–478309; 478311–478313; 478566; *478567; 478568; *478569; 478570; *478571;

478572. *Rhinopoma microphyllum*: AMNH *212070; 236214; *244386; 244387; USNM 294119–294121; *336331; 312221; *312222; 312223; 312226; 312229; 429339–429340; *429341; *429342; 429343–429346. *Rhinopoma muscatellum*: AMNH 212067–212069; 244400–244403; FMNH *102144; *102160; *102175; 102177; 111014; 111023; 111031; *111043; 111061; 112572.

Craseonycteridae: *Craseonycteris thonglongyai*: BMNH *77.3009; TNRC 54–3214; USNM 528306.

Emballonuridae: Emballonurinae: *Balantiopteryx io*: AMNH 189505–189513; 214403. *Balantiopteryx plicata*: AMNH 178408; 178412–178413; 214810–214811; 214813; 214815. *Coleura afra*: AMNH 82369; 237325–237327; 237413. *Coromura brevirostris*: AMNH 267070; 267078. *Emballonura alecto*: USNM 495309; 495312–495317; 495320–495322. *Emballonura monticola*: USNM 196586–196588; 196591–196592; 196595–196596;

196599. *Emballonura semicaudata*: USNM 102435; 102438-102439; 102444; 102446-102451; 102453-102455; 283716; 283719. *Mosia nigrescens*: USNM 277126-277127; 538430; 538432; 545085. *Peropteryx kappleri*: AMNH 265990-265992; 265996; 265998-265999; 265001; 265004; 267081-267082; 267086. *Peropteryx leucoptera*: AMNH 266011; 266013; 267087. *Rhynchonycteris naso*: AMNH 265988. *Saccopteryx bilineata*: AMNH 265963; 265965; 267058; 267060; 267062. *Saccopteryx leptura*: AMNH 265968; 265972. *Taphozous georgianus*: USNM 578483; 578486. *Taphozous mauritanus*: USNM 518618-518620. *Taphozous melanopogon*: AMNH 237718; 237722-237726; 237728-237729; 237732; 241551. *Taphozous perforatus*: AMNH 49357-49358; 82342; 184494; USNM 312270-312274; 312278; 312283; 312288; 312290-312291; 312293; 312295-312296; 312300; 312303; 312306; 312308; 312310; 312313. *Saccolaimus peli*: USNM 463476; 481705. *Saccolaimus saccolaimus*: USNM 501503-501505. **Diclidurinae**: *Diclidurus albus*: FMNH 69366; 88234-88235; USNM 490752. *Diclidurus scutatus*: USNM 490755.

Nycteridae: *Nycteris arge*: AMNH 49387; 86864; 86867; 86912-86913; 170181; 233875-233877; 236295. *Nycteris gambiensis*: FMNH 42191-42194; 42196-42197; 42201; USNM 478628-478632; 478634; 478637; 478639; 478643-478645; 478647-478654; 478661-478662. *Nycteris grandis*: AMNH 237417-237418; FMNH 55741. *Nycteris hispida*: AMNH 49368; 49390; 49392-49394; 49397-49398; 49417; 82387-82388; 89452; 118518; 120307; 120326; 150173; 150183-150184; 170180; 184481-184487; 184500; 184505; 184520-184521; 184524; 184526; 184528; 184530; 217041; 236296. *Nycteris javanica*: FMNH 109315; 141566; USNM 154682; 154686-154687; 154867; 154869; 154871; 563254. *Nycteris macrotis*: AMNH 49422; 89448; 237415; 238281; USNM 478992-478999; 479001. *Nycteris nana*: FMNH 66467. *Nycteris thebaica*: AMNH 188270-188271; 184522; 245153-245154; 257155; USNM 463478; 478932; 479059-479061; 479063. *Nycteris tragata*: AMNH 216803; 233995-233996; USNM 115495. *Nycteris woodi*: USNM 462726; 462731.

Megadermatidae: *Megaderma lyra*: AMNH 236215; *244941; FMNH 65986-65990; 96290-96291; 98233; 102268; USNM 448815; 548635-548636; 548652. *Megaderma spasma*: AMNH 113773; *113774; 187886; *187887; *216804; 216805; 219726; *225547; *225548; 225549; 226850-226851; 233997; 233999; *234000; *234002; *247253; USNM 153881. *Macroderma gigas*: AMNH 162672-162674; *197210; *236544; 236545; USNM *396867; *396894; *396878;

*578488. *Lavia frons*: AMNH 49382-49384; *49420; 82262-82263; 82345-82347; *82348; *82349; *82350; *82385; 82386; 83389; *83390; 170186; 184510; *184511; *184512; 184513; *184514; *184515; 184516-184517; 208789; 219724-219726. *Cardioderma cor*: AMNH 48055; 205337; *219723; FMNH *66662; *68045; *68047; 68051; 68055; 79589; 86594; 86596; 86598; 99547; USNM 462734; *462735; *462736; 462737; *462738; *462739; 497715; *497716; *497717; 497718; *497719; 497720.

Rhinolophidae: **Rhinolophinae**: *Rhinolophus acuminatus*: AMNH *27380; *27381; 27382-27383; *236198; 236199; USNM 254766; 254771. *Rhinolophus affinis*: AMNH *27379; *48026; *55948; 55949; *55950; *61590; 61592; 85239-85240; 85249; *85250; *85251; 85252-85253; *85254; *85255; 85256; 85261; 85269-85270; *236200; 247273. *Rhinolophus alcyone*: USNM *546972; *546978; 546981; *546985. *Rhinolophus arcuatus*: *AMNH 206737; USNM *575055; 575056-575062; *575063; 575064-575068. *Rhinolophus blasii*: AMNH 48077-48078; *119651; USNM *476886. *Rhinolophus borneensis*: AMNH 237751-237752; *257753; 257754-257755; *237756; *237757; 237758; 237761; *237762; *237763; *237765; 237768-237770; *237771; *237772; 237774; *237775; *237776; 237778. *Rhinolophus canuti*: AMNH 237779-237782; 237788-237792; 237794-237801; 237803-237808. *Rhinolophus clivosus*: AMNH *219727; 219728-219732; 244298; USNM 312417-312418; 312449; 312506-312511; 312852-312853; 312855-312857; *462744. *Rhinolophus coelophyllus*: AMNH 216850-216852; *216853; 216854-216855; 216858; *216859; 216860; 216862. *Rhinolophus cornutus*: AMNH 115630; 215728-215733; 215735-215737; *215739; *215770; *215771; *215772; *215773; *215774; *215775; *215776; *215777; *215778; *215779; *215780; 215781; *215782; *215783; 215784; 215786; *215787; 215788; *215789; 215790; *215791. *Rhinolophus creaghi*: AMNH *202248; 202249. *Rhinolophus darlingi*: AMNH 188272; USNM 479221; *479222; 479223; *479224; 479225; *479226; 479228; *479229; 479230; *479231; 479232-479233. *Rhinolophus deckenii*: AMNH *208339; *208340; *208341; *248342; 208343. *Rhinolophus denti*: USNM 322840. *Rhinolophus eloquens*: AMNH 82391-82393; USNM 184323-184324; *184325; *184326; 184327-182328; *184329; *184330; 184332. *Rhinolophus euryale*: AMNH 27384-27387; 31781; USNM 476887-476899; *476900; 476901-476902; *476903; 476904-476907. *Rhinolophus euryotis*: AMNH 54432; 158461-158463; *158464; 158465-158467; *158468; 158469-158470; *190720; 195243; 195248-195249; *241553; 241554. *Rhinolophus*

- ferrumequinum*: AMNH *45001; *45026; *45032; 233073. *Rhinolophus fumigatus*: USNM 479234-479258. *Rhinolophus guineensis*: AMNH 257045; *257046. *Rhinolophus hildebrandti*: AMNH *216207; 216208; 216210-216212; 219735; 245156-245159; USNM 154590; 166650-166651. *Rhinolophus hipposideros*: AMNH 217025; *217302; 218924; 233074-233076; 244132; 246113; USNM *476920; *476921. *Rhinolophus imaizumii*: AMNH 242437-242443. *Rhinolophus inops*: USNM *459457; 459459; 459461-459462; *459464; 459465-459468; *459569; *459470; *459471; *459472; 459473; *459474. *Rhinolophus landeri*: AMNH 185330; 219733-219734; 237419; *237420. *Rhinolophus lepidus*: AMNH *216876; *216877; 216878-216879; *216880; 216881-216886; *216887; 216888; 216890; *216891; 216892; *216893; 216894-216895; 216898-216899; *216900; 216901-216904; 234064-234069; *234070; 234071-234075; *234076; 234077-234078; *237079; 237080; *234081; 234082-234084; *234085; 234086; 236216; *247283; 247285-247287. *Rhinolophus luctus*: AMNH 45109; 45121; *45123; 47992; 56959; *188305; 234056; 247274; *247276; 247277-247278; *247279; *247280; *247281; *247282; *247310. *Rhinolophus macrotis*: AMNH 56966; 85280; 216865-216866; 216868-216869; *216871; 216872-216873; *234057. *Rhinolophus malayanus*: AMNH 216874; *216875; 234058-234059. *Rhinolophus megaphyllus*: AMNH 158471; *158742; 158473; *158475; 158651-158654; 159971; 159973; *159974; 159975-159979; *159980; 159981; *159982; 159983; 160288-160289; 183510-183514; 193726-193727; *193728; *193729; *193730; 193731-193732; *194230; 194231; 194232; *194233; *194234; 194235; *194237; *220076; *220077; *220078; 221851. *Rhinolophus mehelyi*: AMNH 217026; 246108; USNM 476858; *476859; *476860; 476861; *476862; *476863; 476864; 476866-476867; *476868; 476869-476870; *476871; *476872; 476873; *476874; *476875. *Rhinolophus monoceros*: USNM 294145-294159. *Rhinolophus osgoodi*: AMNH 45044; 45046; 45049-45050; 45052; 45054-45055; *45063; 45065; *45069; 45070; *45073; *45074; 45077-45078; 45081; *45082; 45083-45084; 45086; 45088-45089; 45091; 45096. *Rhinolophus pearsoni*: AMNH 117557-117558; 234061-224063; USNM *102464; *102466; *102467. *Rhinolophus philippinensis*: AMNH *206736; 237811-237813; USNM 459496-459497; *573762. *Rhinolophus pusillus*: AMNH 111257-111258; *111271; 111277; *111294; *111298; *111302; 111305; 112775-112776; *112782; 112784; 112791; 112820-112821; 112823; 112839; 112841; 112850; *112867; 112873; 112886; 112888; *112893; 112896; 112899; *112901; 112902. *Rhinolophus rex*: AMNH 56970; USNM 253371. *Rhinolophus robinsoni*: AMNH 236201. *Rhinolophus rouxi*: AMNH 45045; 45071; 45079-45080; *45085; 45092; 45100; 45102; *47996; *47997; 48006; 48010; *48011; 48012; *48015; *48018; *48019; *48020; *48022; 48028; *48029; 48030; 56944; *56946; 56965; USNM 584638-584644; 548654-548660. *Rhinolophus rufus*: USNM 459498; *459499; 459500-459501; *459502; 573588; 574824. *Rhinolophus sedulus*: AMNH 247288; *247289; *247290; 234088-237090. *Rhinolophus shameli*: USNM 528309-528312. *Rhinolophus simplex*: AMNH 54861-54862; *54863. *Rhinolophus simulator*: AMNH *245213. *Rhinolophus steno*: AMNH *216935; *216936; 232526; *232527; 232528; *234103; 247291-247293; *247294; 247295-247299. *Rhinolophus thomasi*: USNM 142553; *142554; *258019; 260167; 528314; *528315. *Rhinolophus trifolius*: USNM 83525; *83573; 84494; 113168; *141091; 142384; *152090; 153960; *153961; *153962. *Rhinolophus virgo*: USNM 101967; 459503; *459504; 459505; *459506; *459507; 459508-459509; 463869-463870; 463872-463875.
- Rhinolophidae: Hipposiderinae:** *Anthops ornatulus*: AMNH 99908. *Asellia tridens*: FMNH *44452; 47763; 67642; 75790; 102443; 111232; 143979; 144004; 144026; USNM 154964-154966; *154967; *154968; 154969; *154970; 154971-154973; 154975; *375915; 448825-448831; 476922-476924. *Aselliscus stoliczkanus*: AMNH 119464-119465; FMNH 38979-38980; 38982; *38985; 38987-38988; *38990; 38991; USNM 528316-528317; 540839. *Aselliscus tricuspidatus*: AMNH 79911; 87125; *144919; *190732; 195244-195245; *195246; 220072; 222754-222756; FMNH *54795; 54796-54798; 54800; *54801; *54802; 54803; 55269. *Cloeotis percivali*: USNM *154589; 238100. *Coelops frithi*: AMNH *115629; 215854; *215855; USNM *358844; 358846; 358859; *358853; *358854; 358855; *358858; 358862-358865; *358866; 358867-358874; *358875; 358876. *Hipposideros armiger*: AMNH *112768; *112769; USNM 578620; *578621; 578622; *578623; 578624; 578649. *Hipposideros ater*: USNM *304407; 304408; *304409; 304410; *304411; 304412; *304413; 304414-304416; 459394; *459395; 459396; *459397; *459398; 459401; *459402; *459403; *459404; *459405. *Hipposideros beatus*: USNM 514675-514676. *Hipposideros bicolor*: AMNH 21695; USNM *18485; 114831; *237956; 237961; 237964; *284169. *Hipposideros caffer*: USNM *479269; *479270; 479271-479274; *479284; 479291-479295; *479296; 479297; *479298; 479299-479300. *Hipposideros calcaratus*: AMNH 99844; 99904; USNM *18480. *Hipposideros cineraceus*:

USNM 241183; 260169-260172; *356211; *356212. *Hipposideros commersoni*: AMNH *237333; *237334; USNM 322844-322853; 375914; *347412; 347413; *347414; 347415; *479422; 479423; *511950; *578855. *Hipposideros cyclops*: USNM *102512; 220900; *220901; 237223-237226; *479424; 479425-479426; 511915-511953; 547002; *547003. *Hipposideros diadema*: AMNH *79876; 79877-79878; *79879; 79880; *79881; 79882; *79883; 79884-79886; 85185-85186; 87145; 87163-87165; 187908-911; *187913; 188307; *194439; 194440-194442; 196646; *202247; 216964; 221852; 232530; 234148-234151; *234153; 234153-234156; *241813. *Hipposideros dyacorum*: USNM 145692; *145693; *145694; *145695; 145696; *145697; 145698. *Hipposideros fuliginosus*: AMNH 236302; *236303; *239396; *239397; *257050. *Hipposideros fulvus*: AMNH 174288; *208110; 208128; *208129; USNM 14534; 187269; *187270. *Hipposideros galeritus*: AMNH 216965; *216966; *234157; 247356; 247383. *Hipposideros jonesi*: USNM 479427-479428; *479429; 479430; *479431; 479432; *479433; 479434-479436. *Hipposideros lamottei*: AMNH 237425; 241098. *Hipposideros lankadiva*: AMNH 236217. *Hipposideros larvatus*: AMNH 234171-234172; USNM 152076; *152077; 152078-152080; *152081; *152082; 152083-152087; *152088; *152089. *Hipposideros maggietylora*: AMNH *196713; 196714-196715; 198622-198624; *198625; 198626-198627. *Hipposideros megalotis*: USNM 375923. *Hipposideros muscinus*: AMNH 108605; 108680; *108681; 108683-108684. *Hipposideros obscurus*: USNM 459430-459431; *459432; *459433; 459434; *459435; 459436; *573280; 573281; 574831. *Hipposideros papua*: USNM *538436. *Hipposideros pratti*: USNM *240238; 240239-240243; *238944; *238950; 238954; 260110-260111. *Hipposideros pygmaeus*: USNM 101975; 101979; 175832; *175833; *175834; 175835; 459438; *459439; *459443. *Hipposideros ridleyi*: USNM 398587-398588. *Hipposideros ruber*: USNM 166395; 166397-166399; *166400; 166401; *166402; 166403; *166404; *166405; 166406-166409; 166412-166413; 166416; 166418-166421; 166423; 166425; 166427; 166430. *Hipposideros sabanus*: AMNH *234175; 236197. *Hipposideros semoni*: AMNH 154856; USNM 553716. *Hipposideros speoris*: AMNH 241501; 241503-241504; *241505. *Hipposideros stenotis*: AMNH 183563. *Hipposideros turpis*: AMNH 241457-241458; 247413; 241459; *241460; 241461; *241462; 241463. *Rhinonictis aurantia*: AMNH 199979; *199980; USNM 284166. *Triadenops persicus*: AMNH 237335-237336; 237328-237340; 245393-245397;

*245398; *245399; *245400; *245401; *245402; *245403.

Vespertilionidae: "Nyctophilinae": *Antrozous dubiaquercus*: USNM 512750-512756. *Antrozous pallidus*: AMNH 21593; 25938; 239590; FMNH 14699; 14701; 14706; 14708; 64593; 64595; 83465; 85519; USNM 6143-6144; 6148; 80714; 81622-81628; 101399; 131933; 131935-131937; 931939; 204010-204017. *Pharotis imogene*: AMNH 160266. *Nyctophilus arnhemensis*: AMNH 216685; 222760; FMNH 120265; 120677. *Nyctophilus geoffroyi*: AMNH 160246; 160306; 197277-197278; 220091; 236781-236786. *Nyctophilus gouldi*: AMNH 66146; 108682; 160319; 216686-216687. *Nyctophilus microtis*: AMNH 192261. *Nyctophilus walkeri*: USNM 369895-369897. **Vespertilioninae:** *Eptesicus furinalis*: AMNH 266371; 267236; 267238. *Myotis nigricans*: AMNH 267222-267229; 267231. *Myotis riparius*: AMNH 267232-267233. **Miniopterinae:** *Miniopterus australis*: AMNH 156903. *Miniopterus magnater*: AMNH 112754; 192553-192555. *Miniopterus minor*: AMNH 237343. **Murinae:** *Murina cyclotis*: USNM 573773; 577777. *Murina florum*: AMNH 192251; 223020. **Kerivoulinae:** *Kerivoula papillosa*: AMNH 247577; 247579-247580. *Kerivoula papuensis*: AMNH 155403. **Tomopectinae:** *Tomopectas rarus*: USNM 103929.

Myzopodidae: *Myzopoda aurita*: USNM 449282; 449284-449285; 449315; 578856.

Molossidae: *Molossus ater*: AMNH 267265; 267267; 267273. *Molossus molossus*: AMNH 267242-267247; 267249; 267252-267260; 267262.

Mystacinae: *Mystacina robusta*: AMNH 160269; USNM 573775.

Thyropteridae: *Thyroptera tricolor*: AMNH 266348; 266350; 266354; 266356; 266358; 266360; 266362; 266364; 267216-267218.

Furipteridae: *Furipterus horrens*: AMNH 265977; 266371.

Natalidae: *Natalus lepidus*: AMNH 186983. *Natalus stramineus*: AMNH 185046.

Mormoopidae: *Mormoops megalophylla*: TTU 12829. *Pteronotus fuliginosus*: FMNH 93671. *Pteronotus personatus*: FMNH 65137.

Noctilionidae: *Noctilio leporinus*: AMNH 265974.

Phyllostomidae: Desmodontinae: *Desmodus rotundus*: AMNH 267211; USNM 494635-494636; 494752; 494760; 494761; 579680. *Diaemus youngi*: USNM 399564. **Phyllostominae:** *Chrotopterus auritus*: AMNH 267131. *Macrophyllum macrophyllum*: AMNH 266039. *Macrotus californicus*: USNM 514038-514039. *Macrotus waterhousii*: USNM 510208-510209. *Micronycteris brachyotis*: USNM 563261-563262. *Mimon crenulatum*:

- AMNH 267114-267115. *Phyllostomus discolor*: AMNH 267116; 267118; 267120-267123; 267126. *Phyllostomus elongatus*: AMNH 266056; 266062-266064. *Phyllostomus hastatus*: AMNH 266071-266073. *Tonatia bidens*: AMNH 266045. *Tonatia brasiliense*: AMNH 267103-267104. *Trachops cirrhosus*: AMNH 266081. **Brachyphyllinae**: *Brachyphylla cavernarum*: USNM 544863-544865. *Brachyphylla nana*: USNM 539779. **Phyllonycterinae**: *Erophylla sezekorni*: USNM 540761-540762. *Phyllonycteris poeyi*: USNM 216678; 216680-216682. **Glossophaginae**: *Anoura geoffroyi*: UMMZ 108640-108641; 108653; 108655. *Choeroniscus intermedius*: AMNH 266377; 267153. *Choeronycteris mexicana*: UMMZ 77754. *Glossophaga soricina*: AMNH 267137; 267142; UMMZ 111278; 111280; 111294; 111300-111301. *Leptonycteris sanborni*: UMMZ 122936; 122938-122939. **Lonchophyllinae**: *Lonchophylla robusta*: UMMZ 114923; 114928-114930; 114933. *Lonchophylla thomasi*: AMNH 267144; 267147. **Stenodermatinae**: *Ametrida centurio*: AMNH 267275-267276; 267278. *Artibeus cinereus*: AMNH 266270; 266265-266266; 267197. *Artibeus concolor*: AMNH 266269; 267194. *Artibeus jamaicensis*: AMNH 266329-266331; 266333-266337; 266339; 266343-266344. *Artibeus lituratus*: AMNH 267203-267205. *Artibeus obscurus*: AMNH 266275. *Chiroderma trinitatum*: AMNH 267186. *Platyrrhinus helleri*: AMNH 267180; 267182. *Sturnira lilium*: AMNH 266226; 266229; 266231; 266234; 266236; 267167-267168. *Sturnira tildae*: AMNH 266248; 266250-266252; 267170. *Uroderma bilobatum*: AMNH 267172-267173; 267177-267178. **Carollinae**: *Carollia perspicillata*: AMNH 266128; 266138-266139; 266143-266144; 266151; 266154; 266162; 267155. *Rhinophylla pumilio*: AMNH 266168-266169; 166173; 266176-266177; 266184; 266188-266189.

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